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TULANE STUDIES IN GEOLOGY AND PALEONTOLOGY

Volume 27, Numbers 1-4 January 31, 1995

AN ONTOGENETIC APPROACH TO UNDERSTANDING CHANGES IN SHELL MORPHOLOGY OVER TIME: THE *STROMBUS ALATUS* COMPLEX IN THE PLIO–PLEISTOCENE OF SOUTHERN FLORIDA

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TULANE STUDIES IN GEOLOGY AND PALEONTOLOGY

Volume 27

1995

HUBERT C. SKINNER

and

EMILY H. VOKES

Editors

TULANE UNIVERSITY OF LOUISIANA
New Orleans

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TULANE STUDIES IN GEOLOGY AND PALEONTOLOGY

BIOSTRATIGRAPHY AND EVOLUTION IN THE COASTAL PLAIN

A SYMPOSIUM PRESENTED MARCH 20, 1991
WINSTON SALEM, NORTH CAROLINA

WARREN D. ALLMON, EDITOR

TULANE UNIVERSITY OF LOUISIANA
New Orleans

VICTOR AUGUST ZULLO
1936-1993

Victor Zullo ("Vic" to almost everyone) was born in San Francisco and completed his entire college education at the University of California, Berkeley, where he first developed his interest in barnacles. Although his training was as a paleontologist, his early work experience was primarily as a marine biologist, and his initial position at the University of North Carolina, Wilmington, was as a Professor of Biology and Director of the Program in Marine Studies. But after two years, in 1973, he moved to the Department of Earth Sciences and began to develop his life-long interest in the geology, stratigraphy, tectonic history, and geomorphology of the Atlantic Coastal Plain. In the ensuing years he served as an inspiring and beloved teacher and dedicated researcher, leaving behind a legacy of nearly 70 studies on the Cirripedia, plus another 20 papers on Coastal Plain stratigraphy. (*From* W.B. Harris, 1993, American Paleontologist, volume 1, number 5).

INTRODUCTION

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Most of the papers assembled in this issue originated as presentations in a Symposium held at the annual meeting of the Southeastern Section of the Geological Society of America in Winston-Salem, North Carolina, March, 20, 1991. The title sounds so general as to seem meaningless, yet it was chosen on purpose. Although the first published figure of a fossil from the New World was a Neogene mollusk from the Atlantic Coastal Plain [*Chesapecten jeffersonius* (Say), figured by Lister in 1687; see Ward and Blackwelder, 1975, U.S. Geol. Survey, Prof. Paper 861], and a great deal of attention has been paid to the description of mollusks and other fossil macro-and microfauna of the Coastal Plain since that time, the truth is that we are woefully ignorant about most of the basic biostratigraphic and evolutionary patterns of the marine faunas of the last 65 million years in what is now the region between the Potomac River and the Rio Grande. Despite an apparently widely-held belief among many (mostly non-Coastal Plain) geologists and paleontologists that the most basic descriptive work in the Coastal Plain has "been done," there remains a need for careful studies of the patterns of occurrence of these abundant, diverse, and well-preserved fossils. Only when such work has been carried out can studies of the evolution of phylogenetic lineages, biogeographic distributions, and depositional basins (which are usually viewed as "more interesting") be accomplished.

The papers in this issue represent steps in several of these directions, using several different approaches and groups of organisms. They show the scope of the need for more work, both in basic description and in evolutionary and stratigraphic interpretation. They also show that there remain profound controversies to be resolved in this long-studied part of the world.

This issue is dedicated to the memory of Victor A. Zullo. Vic was a leader in the paleontological and geological study of the Coastal Plain, and his presence is sorely missed by those who knew him and his work. Vic also made a presentation at the Symposium (with Roger Portell) entitled: "Caught in the act: derivation of a pyrgomatid coral barnacle from an archaeobalanid ancestor."

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AN ONTOGENETIC APPROACH TO UNDERSTANDING CHANGES IN SHELL MORPHOLOGY OVER TIME: THE *STROMBUS ALATUS* COMPLEX IN THE PLIO-PLEISTOCENE OF SOUTHERN FLORIDA

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I. ABSTRACT

The study seeks to focus upon the process of shell growth, as well as on the end product of that process, as a way of understanding molluscan shell morphology and how it changes over time. Techniques developed for analyzing individual ontogeny, when applied to the members of a sample, yield a multifaceted mean growth profile for that sample. The growth profiles of multiple samples of the same putative taxon are then compared to obtain a more generalized set of growth patterns for that taxon. Finally, the process is applied to the various members of a fossil lineage to provide insight into changes in the process of shell growth over time.

Presented herein are the results of a detailed ontogenetic study of Recent and fossil material from a number of biostratigraphic horizons in southern Florida involving the mesogastropod subgenus *Strombus* sensu stricto, a common component of the shallow-water marine fauna. Evidence from this study indicates that *Strombus floridanus* Mansfield, 1930, the earliest member of the subgenus in the Florida Pliocene, differs from the extant species *Strombus alatus* Gmelin, 1791, in both adult morophological characteristics and patterns of growth, and that the former represents the ancestral form of the latter. *Strombus floridanus* is restricted to the *Cancellaria* zone of the Jackson Bluff Formation in the Florida Panhandle and to the lower Pinecrest beds in southern Florida, whereas *S. alatus* makes its first appearance in the post-Bermont Pleistocene. Connecting these two taxa are a suite of fossil forms representing a single, morphologically changing lineage. Within this lineage growth patterns in the larval stage undergo a series of incremental changes in one direction during this time interval, while growth patterns in the benthic stage and adult morphological features exhibit a complex set of changes, some being incremental and others undergoing a single large-scale transformation at one point in the geologic record.

The transformation from *S. floridanus* to *S. alatus* appears to have taken place over about a one million year interval in the fossil record (from about 2.4 Ma to 1.4 Ma), and has been followed by a period of apparent morphologic stasis. Two intervening morphological forms or chronospecies can be distinguished, separable in their growth patterns and some adult morphological features from the end-point taxa and, to a lesser extent, from one another. With some reservation, *Strombus evergladesensis* Petuch, 1991, and *Strombus lindae* Petuch, 1991, have been accepted as valid names for these two forms. The former, as interpreted herein, ranges from the upper

Pinecrest to the basal Bermont, while the latter is restricted to a higher Bermont horizon. The existence of two clearly differentiable forms in different units of the Pinecrest beds, as exposed in the APAC Pit near Sarasota, supports the hypothesis of a substantial hiatus separating Units 2-4 from the underlying Units 5-10, and suggests that only the lower units are correlated with the Jackson Bluff Formation of northern Florida. The presence of *S. alatus* throughout the section exposed in the Leisey Shell Pits of southern Hillsborough County raises serious doubts about the placement of much of that section in the Bermont Formation.

II. INTRODUCTION

Of the eleven living subgenera of the mesogastropod genus *Strombus*, eight are confined to the Indo-Pacific Province, whereas three have representatives in the New World. Of those three, only members of the subgenus *Strombus* sensu stricto are restricted to the New World. There, three extant species survive. One, *Strombus gracilior* Sowerby, 1825, lives in the Pacific Panamic Province and the other two, *Strombus pugilis* Linnaeus, 1758, and *Strombus alatus* Gmelin, 1791, are found in the Atlantic Caribbean and Carolinian Provinces, respectively.

Throughout much of its range, *S. alatus* is a common component of the shallow-water molluscan assemblage, being present in quiet back bays, on intertidal sand bars, and on sandy substrates to depths of at least 35 meters along the continental margins. Local concentrations of five individuals of mixed age (adults and juveniles in excess of 30 mm) per square meter are not uncommon in intertidal habitats. The species is not present in the Bahamas, but is found 150 kilometers from the mainland in the off-shore atoll/reef areas of the Campeche Bank (Vokes and Vokes, 1983, p. 54).

Fossil members of the subgenus can be found in many Late Miocene, Pliocene and Pleistocene shallow to moderately deep-water, sub-tropical to tropical marine deposits in the New World. In the Pliocene and Pleistocene deposits of southern Florida, members of this subgenus are probably the most common medium-sized gastropods present, sometimes being found *in situ* in dense pockets or layers (Geary and Allmon, 1990).

The form studied by Geary and Allmon, from the lower units of the Pliocene Pinecrest beds (Olsson, 1964 = Fruitville Formation of Waldrop and Wilson, 1990), is generally considered to be *Strombus floridanus* Mansfield, 1930. Although the shell morphology of adult specimens of this taxon clearly differs from that of *S. alatus*, *S. floridanus* is most likely the mid-Pliocene ancestral form of the extant species. Contained in the overlying Late Pliocene and Pleistocene deposits of southern Florida belonging to the upper Pinecrest beds, the Caloosahatchee Formation (Dall, 1887), the Bermont Formation (DuBar, 1974), and the Fort Thompson/Coffee Mill Hammock Formations (Sellards, 1919),[1] is a suite of intervening forms that appears to represent a single lineage spanning some 3 to 3.5 million years.[2] The relative completeness of the fossil record in southern Florida over this period of time, together with the abundance and generally excellent state of preservation of *Strombus* specimens present in that record, make them excellent candidates for a detailed analysis of phylogenetic changes in shell morphology.

III. MATERIALS AND METHODS

Central to the study of fossil molluscan taxa is the need to be able to distinguish expressions of variation within a taxon from the character states that separate taxa. With Recent forms this can be accomplished by carrying out statistical analyses whenever a suitably large sample can be obtained from a single population. However, it is virtually impossible to determine whether fossil specimens, even when collected from the same locale, are members of a single population. Even *in situ* collections are unlikely for a number of reasons to represent a biological community (see Geary and Allmon, 1990). Nevertheless, when samples taken from biological populations of extant taxa are available for comparison, statistical analyses of carefully collected fossil material can yield useful information about probable intraspecific variation.

For work with both fossil and extant taxa, even statistical analyses can lead to misleading conclusions when care is not taken to distinguish between adult and juvenile forms. Within the family Strombidae this need not be a problem since adults can easily be differentiated from their juvenile counterparts. However, to the extent that this causes investigators to focus attention only upon those shell characteristics expressed in the adult stage, potentially valuable insights can be lost. In such instances attention tends to be focused almost exclusively on the last whorl of the teleoconch, and particularly on the form of the expanded and thickened adult lip. While vestiges of the previous whorls (12 to 14 in *Strombus* s.s.) are retained in the adult spire, it is generally only their collective impact in terms of spire shape that is noted. Yet close scrutiny reveals complex sculptural features on these earlier whorls, features that often differ from whorl to whorl. Since these features represent a partial history of the ontogeny of the individual, it would seem to be legitimate, and indeed potentially illuminating, to study their **pattern of development** over the entire protoconch and teleoconch, *i.e.*, to pay as much attention to developmental processes as to the final product. It is this ontogenetic approach to the study of molluscan shell characteristics that is at the core of the present investigation.

The analysis of gross features.

Measures. Several measurements were made of the overall shell dimensions of individual specimens. These are listed below, with the actual measuring protocols outlined in the Appendix.

Shell Length
Maximum Shell Width
Dorsal/Ventral Shell Width
Spire Height

Body Ornamentation. The presence/absence and nature of both axial and spiral sculptural elements on the body whorl of adult specimens were noted. In addition, the presence of any of three spiral sculptural elements sometimes found inside the aperture of adult specimens was noted; submarginate costae along the inside of the lip, short denticles on the anterior columella opposite the stromboid notch, and fine threads or rugosities on the parietal wall near the point of posterior lip attachment. The shape of the expanded adult lip itself was found to be of no value for differentiating taxa within this study.

Color Pattern. Elements of color pattern in Recent and, where still visible either under normal or long-wave (3660 Å) ultraviolet illumination, in fossil specimens were recorded. Of note were the presence and nature of darker axial patterns particularly on the ventral side of the body whorl in adult specimens, together with markings associated with resting varices on the spire.

Ontogenetic analysis.

The types of shell characteristics that lend themselves to an ontogenetic or developmental analysis can be placed in three categories: (1) overall whorl dimensions or shape; (2) the details of axial ornamentation; and (3) the details of spiral ornamentation. Several aspects of the spiral and axial ornamentation can be noted: (1) the onset or cessation of expression of the feature; (2) the number of elements per whorl; (3) the strength or degree of expression of the element on each whorl; and, (4) the nature of the expression of the element (*i.e.*, the overall geometry of expression) on each whorl.

Whorl Dimensions. Three linear measurements were taken for each whorl of a specimen to characterize the process of shell development. These are listed below, with the measuring protocols outlined in the Appendix.

Whorl Diameter
Whorl Height
Shoulder Height

It has been shown that the vast array of gastropod forms can be approximated in computer simulations by manipulating three variables; the shape of the curve representing the body cavity, the exponential rate of expansion in the plane of coiling, and the exponential rate of movement along the axis of coiling.[3] In these computer simulations, the rates remain constant as the "shell" grows.[4] If one were to plot the change in whorl diameter for one of

these computer-generated gastropods as a function of whorl number on a semi-log graph, the result would be a straight line whose slope would represent the rate of spiral increase; for example, low for a *Turritella* and high for an *Architectonica.* Similarly, if one were to plot the change in whorl height and shoulder height for such hypothetical creatures in the same manner, the results would once again be straight lines whose slopes (the same in this case) would represent the rate of translation parallel to the axis of coiling, high for a *Turritella* and low for an *Architectonica.*

To what extent do these computer simulations reflect the ontogeny of real gastropods? By carrying out the whorl-by-whorl measurements listed above for individuals in a sample and then using them to establish mean values for the three growth characteristics, it is possible at least to determine the average behavior of a particular type of gastropod. Text-figure 1 plots the results of such an analysis for a sample of *S. alatus* for each of the three measures. Several points should be noted. First, the plots are close to, but not exactly, straight lines; in the real world, growth rates (*i.e.*, slopes) change over the course of shell development. Second, there is a similar pattern to each of these suites of changes. Third, the timing of the changes is slightly different for each of the three measures. It is the presence and nature of these rate changes that is of potential value in discriminating among different taxa. The questions central to this investigation are, do these developmental patterns differ sufficiently even among closely related forms to be of value in differentiating *Strombus* s.s. from the Florida Pliocene/Pleistocene and, if so, have they changed over time in any consistent manner?

The plots portrayed in Text-figure 1 capture aspects of the growth process but tell little about how the alterations in process give rise the characteristics observed in the finished product – the shell morphology of an adult *S. alatus.* For this purpose it is useful to create a series of curves, hereinafter referred to as **second order curves**, that portray the ways in which these individual characteristics combine with one another over the course of shell development.

Text-figure 2 portrays three such curves. The first of these (A) plots the ratio of whorl diameter to whorl height as a function of whorl number and serves to communicate about the overall shape of the spire. A horizontal plot would indicate a straight-sided spire; the lower the ratio, the smaller the spire angle. A positive slope on this graph is indicative of a concave spire aspect; the greater the slope, the greater the concavity. A negative slope indicates a convex spire aspect. In the case of *S. alatus,* there are a series of early subtle changes ranging over the protoconch and early teleoconch, followed by a transition to a moderately concave spire over most of the teleoconch.

The second curve (B) plots the ratio of whorl diameter to shoulder height and indicates whether the spire whorls appear to be sloping or tabulate; the higher the ratio the more tabulate the whorls. A plot with a positive slope would indicate a spire with an increasingly tabulate aspect and *vice versa.* In the case of *S. alatus,* the trend is towards an increasingly tabulate whorl profile, although the change is moderate and there is a distinct short-term reversal during the early teleoconch whorls and another in the later stages of teleoconch development.

The third curve (C) plots the ratio of shoulder height to whorl height as a function of whorl and indicates whether or not the spire whorls appear to be turreted in outline. A ratio of 0.5 represents a whorl in which the shoulder is situated midway between the sutures, whereas a ratio of 1.0 indicates a whorl in which the shoulder is overrun by the suture of the succeeding whorl. *Strombus alatus* yields a turreted whorl profile throughout with only a slight tendency for the suture of later teleoconch whorls to approach the shoulder of the previous whorl.

Axial Elements. The number of axial elements (ribs, knobs, or resting varices) present on each whorl was recorded and the largest element (excluding resting varices) measured. Also noted were the point at which axial sculpture was begun and the point, where applicable, at which it was terminated. The data collected from individual specimens were combined to establish a set of mean values for each sample

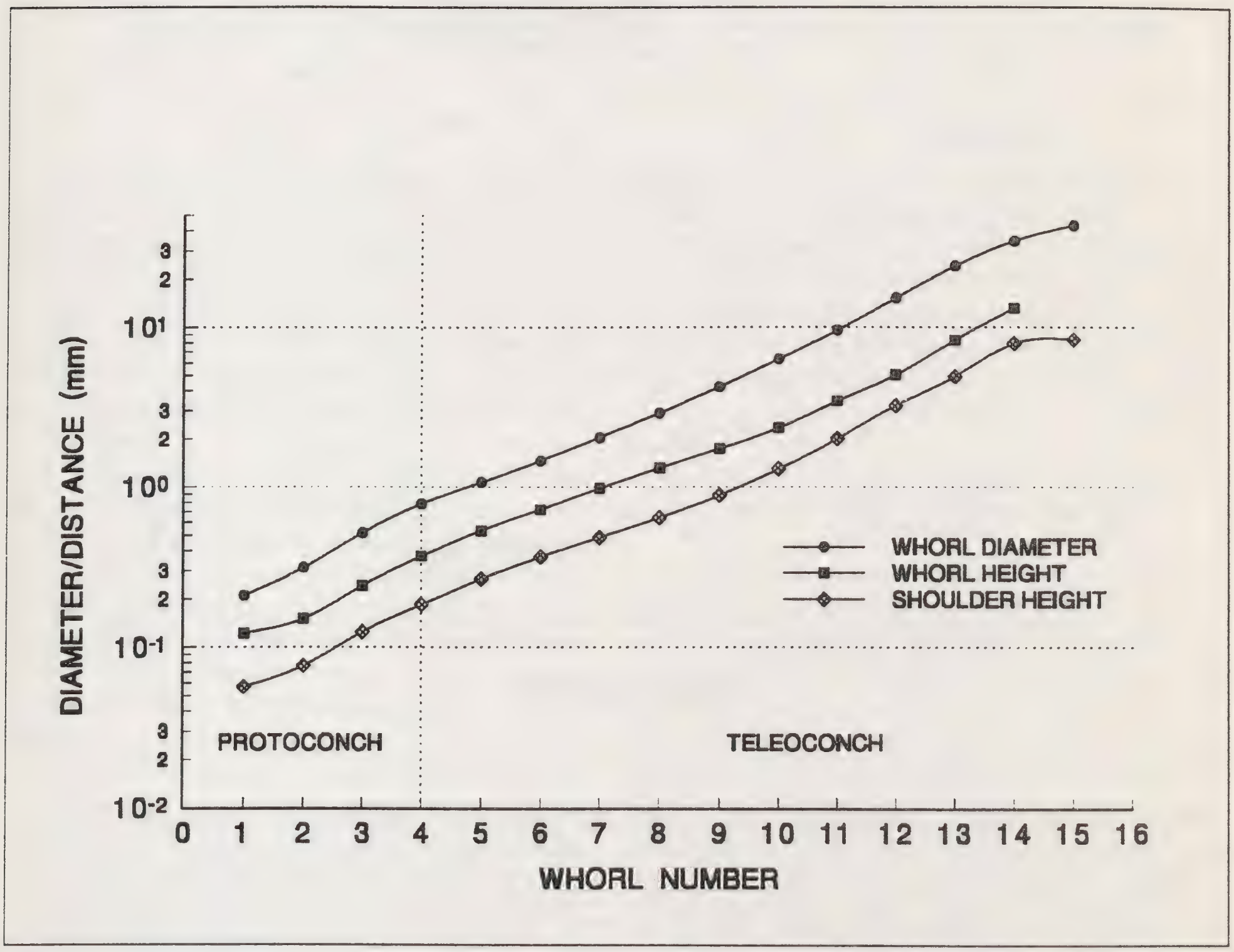
which in turn were plotted. Text-figure 3 shows a pair of such plots for a sample of *S. alatus*, the first of which tracks the growth of axial element size as a function of whorl, and the second of which tracks the total number of axial elements present on each whorl. The second plot can be understood as portraying the relationship between the rate of growth of the axial elements themselves and the rate of growth in whorl circumference (or whorl diameter).

The curves portrayed in Text-figures 1, 2, and 3 represent a mean **growth profile** for the specimens in the sample of *S. alatus* analyzed and, to the extent that this sample can be seen as being representative of the species, as a mean growth profile for the taxon.

Spiral Elements. A number of aspects of spiral sculpture were tracked, but only the point at which spiral sculpture was initiated (or at least became visible above the attachment point of the succeeding whorl) appeared to be significant for this study. The protoconch/teleoconch boundary was defined as that point at which either axial or spiral sculpture was first noted (in those specimens sufficiently well-preserved to observe the onset of sculpture).

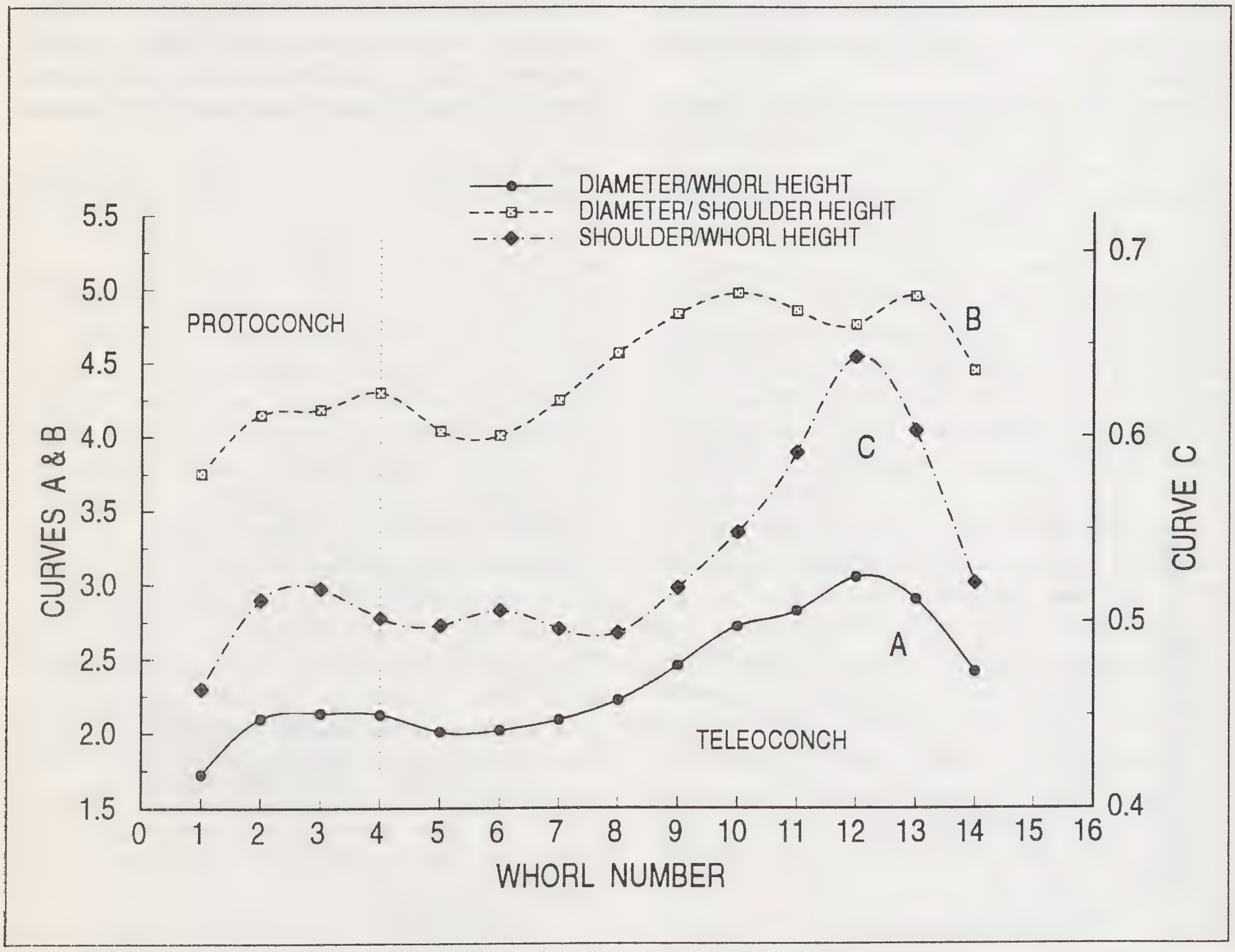
Material analyzed.

Recent *S. alatus* were obtained from five regions within the range of the species: (1) the Florida Keys; (2) southwestern Florida, from Naples to Sanibel Island; (3) St. Andrews Bay in the Panhandle of Florida; (4) Heald Bank, east southeast of Galves-

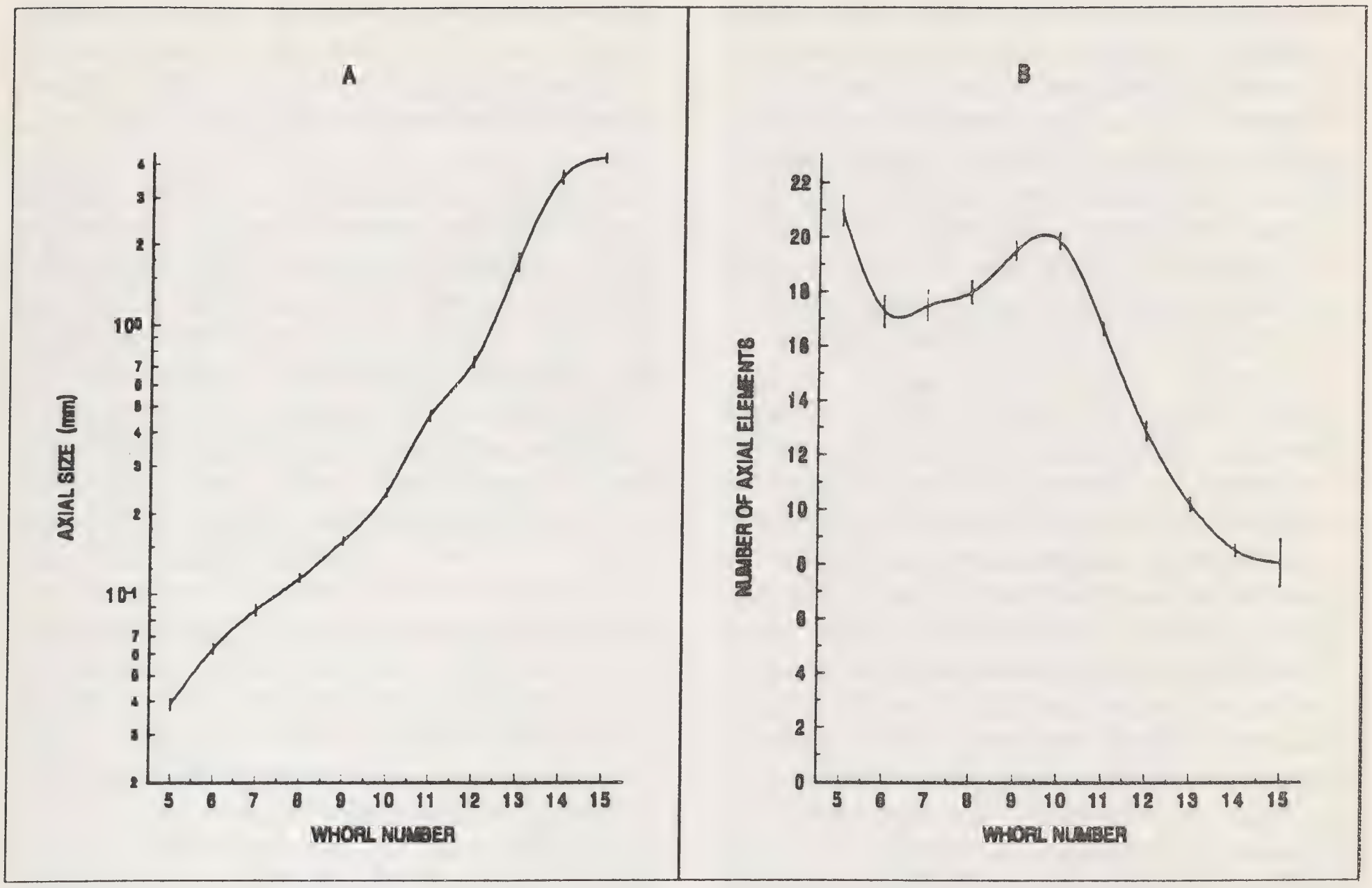


Text-figure 1. Primary growth characteristics for *S. alatus*. Each curve connects the mean values of whorl-by-whorl measurements taken on 73 juvenile and adult specimens from various localities along the Gulf Coast of Florida. The vertical dotted line represents the approximate point of transition from protoconch to teleoconch. Straight line plots would indicate constant rates of growth over shell ontogeny.

ton, Texas; and (5) the Yucatan coastline in the state of Campeche, Mexico. Only the material from St. Andrews Bay (RFG10)[5] and Heald Bank (RTG01) could be said to have come from a single biological population, each being collected from one locality at a single point in time in the 1960's. The southwestern Florida material contains a small sample (RFG01) collected at one time from the Naples area, together with a larger quantity of material (RFG02, RFG03) from Sanibel Island, designated as the type locality for *S. alatus* by Clench and Abbott (1941, p. 8), collected over the past decade. The Florida Keys material contains a number of small lots collected in different locations among the Keys and at different times (RFK01-RFK05). The material from Campeche was collected during three trips within a 21 month period from four different localities along a 135 kilometer stretch of coastline (RCM01-RCM04). The vast majority of these specimens, however, were collected near the middle of that stretch (RCM02) in January of 1993 and 1994. Only the material from southwestern Florida and the Florida Keys contained both adults and juveniles sufficient-



Text-figure 2. Second order growth curves for the same sample of *S. alatus* as in Text-figure 1, representing three distinct pair-wise combinations of the three primary growth measures; whorl diameter, whorl height and shoulder height. Curve A conveys information concerning whether the spire profile is seen as concave, convex, or straight sided, with a positive slope indicating a concave aspect. Curve B conveys information as to whether individual whorl profiles appear to be tabulate or sloping, with a positive slope indicating an increasingly tabulate aspect over shell development. Curve C conveys information concerning the placement of the suture of the succeeding whorl relative to the whorl periphery and, hence, whether a whorl appears to be turreted or embedded. A positive slope here indicates a spire wherein whorl profiles become increasingly embedded with shell development.



Text-figure 3. Curves representing the expression of axial shell ornamentation (ribs, knobs, spines and/or resting varices) over the course of shell development for the same sample of *S. alatus* as in Text-figures 1 and 2. [A] portrays the growth of axial element size (excluding resting varices) with shell development. A straight line plot would indicate a constant growth rate over shell ontogeny. [B] portrays changes in the number of axial elements per whorl (including resting varices) over shell development. In each instance, the curves connect mean values for these data and the short vertical lines indicate the standard error of each mean.

ly well preserved to allow for the construction of complete growth profiles, and even in the latter of these two cases the number of juveniles was small. The Heald Bank sample contained only very small juveniles, but the St. Andrews Bay and Campeche Coast samples were almost exclusively adults with significant spire degradation.

In identifying fossil material for analysis, the goal was to obtain reasonably large samples from each of the major Pliocene/Pleistocene biostratigraphic units of southern Florida. Ideally, one would have liked to have had access to large, randomly collected samples collected *in situ* from a single biostratigraphic horizon. However, this was not always possible even with collections made by the author. Below is an indication of the degree of stratigraphic precision present in samples utilized for the profiles of the morphological forms found in various biostratigraphic units.

Lower Pinecrest Beds. The sample utilized to create the growth profile for the form in southern Florida generally assumed to be *S. floridanus* was composed of material taken *in situ* from two localities about two kilometers apart in the northern part of Sarasota County, the APAC pit (TU 1000) and Phase 6 of the Quality Aggregates operation (TU 1524) immediately to the east (see map in Geary and Allmon, 1990, p. 260). The APAC material was taken from the bottom of Unit 7 as designated by Petuch (1982), and the Quality Aggregates sample from the corresponding unit (*i.e.*, just above a bed of *Vermicularia recta* Olsson and Harbison, 1953, that underlies Unit 7 over extensive areas in both pits).

Jackson Bluff Formation. Strombus floridanus, collected from the type locality and nearby Jackson Bluff localities in northern Florida, was also analyzed. This material represents several rather small lots in the Florida Museum of Natural History and the Tulane University collections from different localities in Leon and Gadsden Counties collected over a number of years (TU 60, GD003, LN001-LN004).

Upper Pinecrest Beds. The material utilized in developing the profile of the form found in these units was collected once again from the APAC pit and Phase 6 of the Quality Aggregates operation in northern Sarasota County. The APAC material was taken from Petuch's Units 4 and 2. The Quality Aggregates specimens came from the unit equivalent to Petuch's Unit 4, and from a higher unit containing substantial numbers of *Trochita floridana* Olsson and Petit, 1964. Lyons (1990) considers this bed to be intermediate between Unit 1 at APAC, which he contends is Caloosahatchee in age, and Unit 2, the uppermost Pinecrest unit at APAC. Although all specimens appear to have been *in situ*, the areas collected had been disturbed by the removal of overburden. This resulted at both sites in the exposure of significant lateral expanses of the rather thin Unit 4, grading upwards into Unit 2 at APAC. The *Trochita* bed was exposed as a cut beside a road running along the east wall of the Phase 6 pit at Quality Aggregates, together with a sloping surface above the road cut.

Caloosahatchee Formation. Material utilized for this profile was collected from the De Soto Shell Pits in southern De Soto County (TU 1512). Over the years several pits have been dug by the same mining company over an area of about four square kilometers. The specimens utilized in this study came from pits 2 and 3, about 16 kilometers south of Arcadia. Although the pits were pumped during extraction of the marl, *Strombus* specimens were not plentiful enough to make an *in situ* collection from a single horizon. The specimens used for this analysis were collected both from spoil and *in situ* from various horizons within the two pits. Inspection of *in situ* material did suggest that a Caloosahatchee fauna was present everywhere except at the very top and possibly the very bottom of pits 2 and 3.[6] Care was taken to collect only those spoil specimens found in association with Caloosahatchee index fossils.

Bermont Formation. DuBar (1974) suggested the name Bermont Formation for the uppermost marine beds along Shell Creek in Charlotte County (TU 539A) and included within this new biostratigraphic unit exposures at Ortona Lock on the Caloosahatchee Waterway and at various localities south and east of Lake Okeechobee informally referred to by Vokes (1963) as the "Glades formation" and by Olsson (1964) as "Unit A." While sites north and west of Lake Okeechobee have, at times, allowed *in situ* collecting of Bermont material, the sites south of Lake Okeechobee that have yielded species identified by DuBar as Bermont indicators [*i.e., Anadara aequalitus* (Tucker and Wilson, 1933), *Strombus mayacensis* Tucker and Wilson, 1933, *Fasciolaria okeechobensis* Tucker and Wilson, 1932, *Fusinus watermanni* (M. Smith, 1936), *Melongena bispinosa* (Philippi, 1844), and *Vasum floridanum* McGinty, 1940] have all been worked with drag lines in an environment where the water table is essentially at the surface. Unfortunately, these drag lines have also usually brought up material of probable Caloosahatchee age, as well as younger material belonging to the Ft. Thompson or Coffee Mill Hammock Formations.

Although it was possible to obtain a small sample of *Strombus* from the type locality for study, the specimens were deemed too few and too poorly preserved to provide an adequate profile. Aside from the Leisey Shell pits in Hillsborough County (HI001, HI013-HI015), whose Bermont age placement appears to this investigator to be questionable, this was the only *in situ* Bermont material available at the time of the study. Abundant spoil-collected material from several localities south and east of Lake Okeechobee (TU 201, TU 580, TU 978) was available, though it could not be determined with certainty that the samples analyzed from any of these sites were strictly Bermont in age. Chosen for purposes of creating a Bermont profile are specimens collected about 18 kilometers south of South Bay in Palm Beach County from spoil piles along the North New River

Canal produced in the early 1980's when that waterway was being deepened (F07). Petuch (1991) claims that these excavations were being made to a depth of 15 meters, but does not indicate the original canal depth prior to this work. At the locality collected, Bermont but no Caloosahatchee indicator fossils were found. This sample is compared with another from the Star Ranch pit (TU 1536) about one kilometer to the southwest where the excavation has brought up Caloosahatchee as well as Bermont indicators, most notably *Contraconus tryoni* (Heilprin, 1886), *Echinofulgur echinatum* (Dall, 1890), and *Siphocypraea problematica* (Heilprin, 1886).

Post-Bermont Units. Material utilized to generate this profile came from two excavations in Lee County and a third in Palm Beach County. The first site is a ditch dug to a depth of four to five meters just to the north of the South Florida Mining pit on County Road 765 about five kilometers (three miles) south of the Charlotte County/ Lee County border (F15). A second lot of material, taken from a temporary excavation at the site of a new hospital between Fort Myers and Fort Myers Beach (F11), was given to the author by an amateur collector. The depth of this excavation was not recorded. The third lot comes from spoil piles associated with irrigation canal work along the south side of Florida Route 80, northeast of Belle Glade (F14). Once again the depth of the excavation is unknown. At all three sites *Strombus* specimens were the dominant faunal element and there were no indicator fossils for Bermont or older horizons. While it is clear that the material in each case came from the uppermost horizon at that locality and that that horizon was probably younger than Bermont in age, it has not been possible to assign the horizons to any specific post-Bermont unit (either the Coffee Mill Hammock Formation or the supposedly underlying Fort Thompson Formation) with certainty. For a discussion of the possible relationship between these two later Pleistocene units see Lyons (1991, p.159-161).

Experience has taught the author that specimens of fairly common species in private collections have often been kept because of their "unusual" size or appearance, thereby frustrating attempts to uncover typical morphological characteristics. Hence, whenever possible specimens collected by the author were utilized for analysis so as to avoid these potential collecting biases. In some instances all specimens encountered were taken. In other instances, where the wealth of material allowed some selectivity, fragments and specimens too worn to yield useful information were left behind. Nonetheless, some bias undoubtedly did show up in the analysis itself. The gross features were recorded for at least all adults in each collected sample. However, the development of growth profiles requires specimens possessing clean, uneroded, reasonably complete spires wherever possible. These criteria introduce a bias in favor of juvenile specimens and young adults over more mature adult specimens. It also introduces a bias in favor of specimens that had lived in comparatively low energy environments. In many instances all specimens in the lot exhibited significant spire wear but unworn body whorls, indicating that they had probably lived in a fairly high energy environment (*e.g.*, on intertidal sand bars rather than on a back bay sand/grass flat). The specimens in other lots showed overall shell wear suggesting a beach assemblage or post-depositional weathering. In those cases, the specimens retaining the most complete information were utilized in creating the growth profiles.

IV. RESULTS AND DISCUSSION

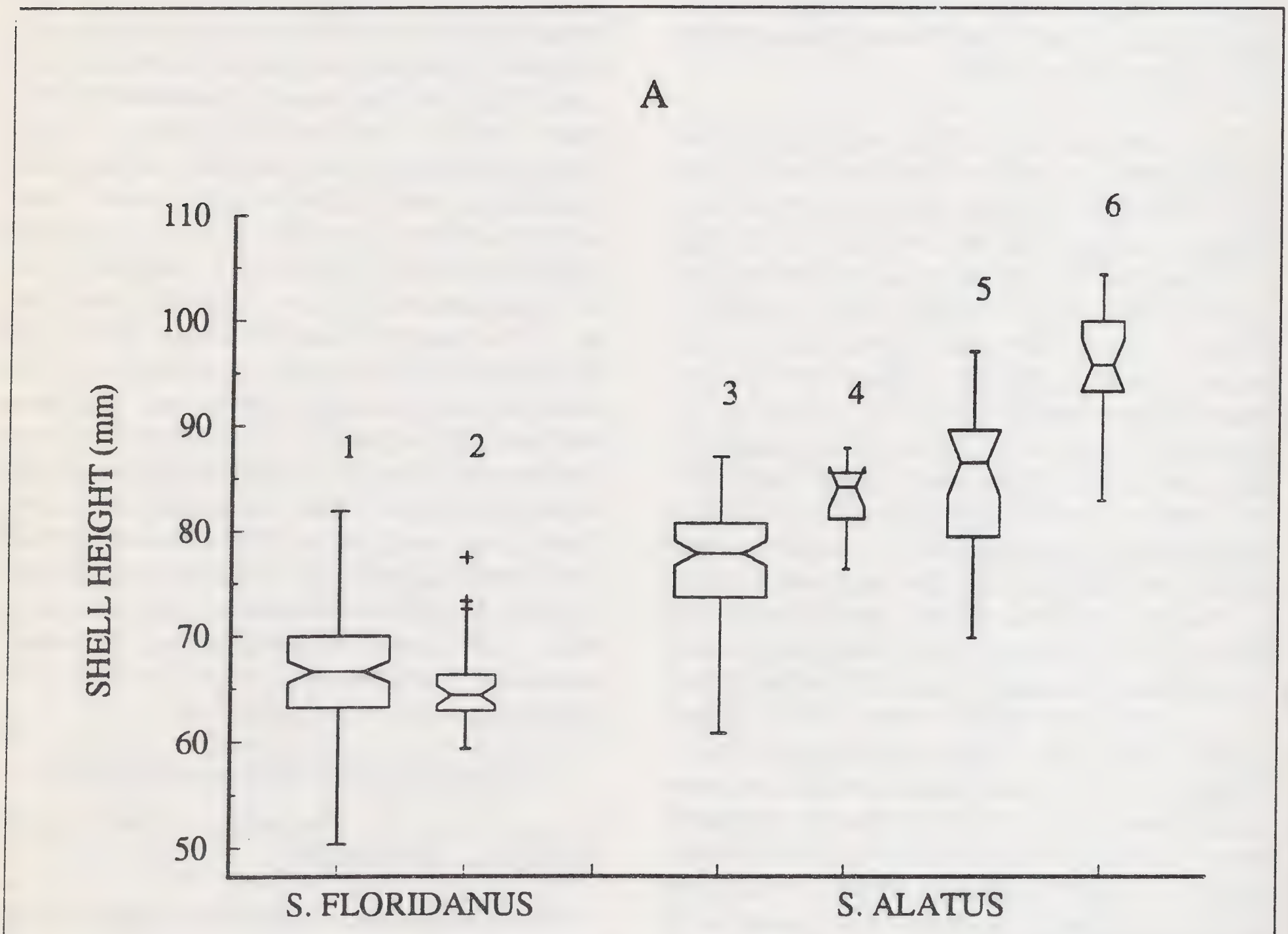
Comparison of *Strombus alatus* and *Strombus floridanus*.

The fossil record in southern Florida is a rich one from the middle of the Pliocene onward. In it, *Strombus floridanus* represents the earliest known apparent ancestral form of the Recent *Strombus alatus*. A comparison of these taxa, separated in time by some 3.0 to 3.5 million years, is a necessary first step in the analysis of morphologic change in Florida *Strombus* over time. When Mansfield described *Strombus floridanus* as a new subspecies of *Strombus pugilis* in 1930, he noted three characteristics that served to distinguish it from another assumed subspecies of *Strombus pugilis*, the Recent *Strombus pugilis alatus*:[7]

> "The new subspecies is closely related to *Strombus pugilis alatus* Gmelin but differs from the latter in having a shorter shell with a lower and less turrited [*sic*] spire, and fewer nodules or tubercles. In the new subspecies, the suture winds upon or above the spiral row of tubercles except on the earliest whorls and on the last half of the body whorl. On *S. pugilis alatus* the suture falls below the tuberculate shoulder." (Mansfield, 1930, p. 95)

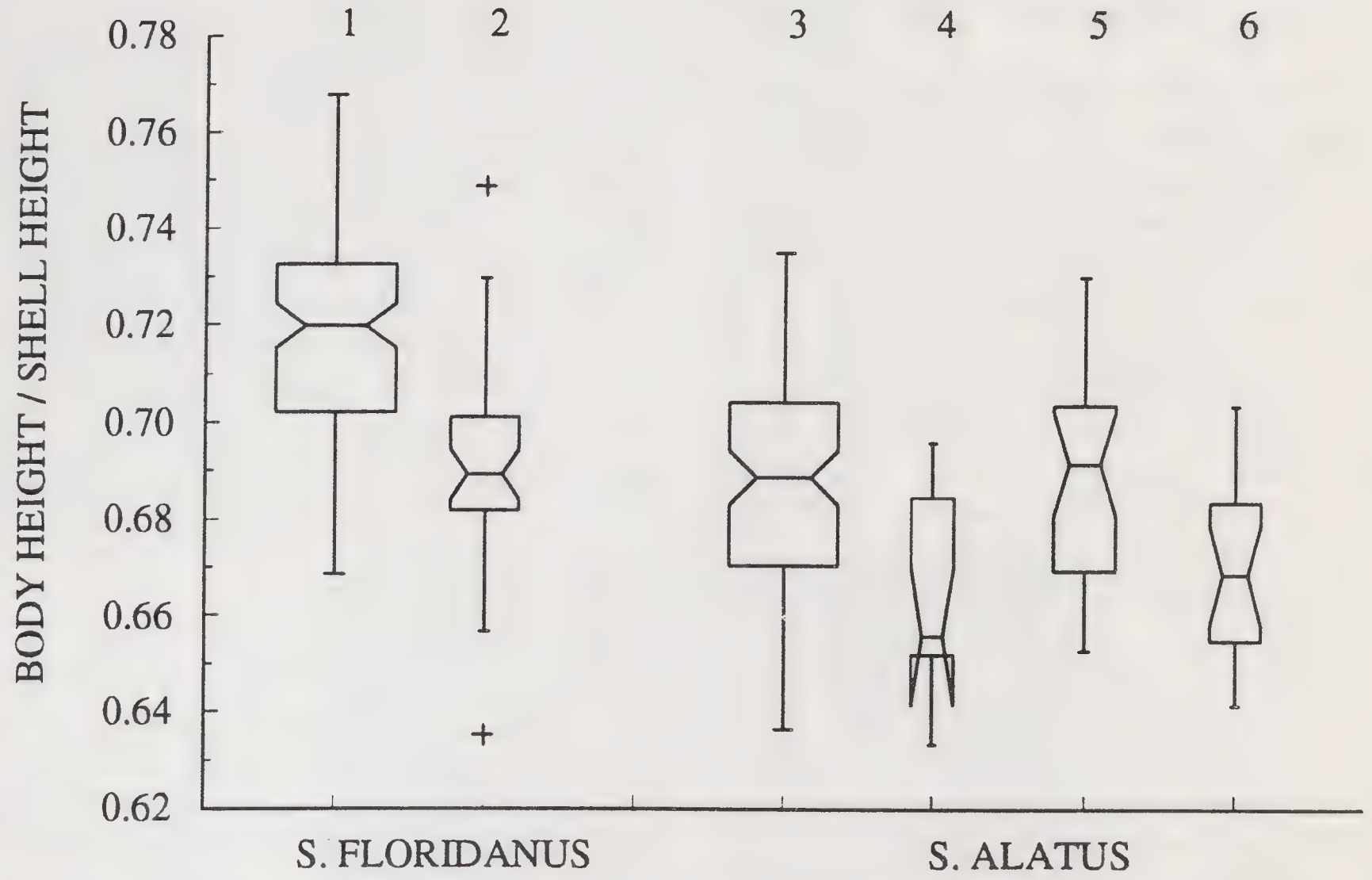
In addition, he noted the presence of a distinct color pattern on the body whorl of *S. floridanus,* but did not compare this feature with the patterns found among specimens of *S. alatus.*

The material analyzed by Mansfield was from the Jackson Bluff Formation (Puri and Vernon, 1964 = the *Ecphora* and *Cancellaria* zones of the Choctawhatchee Formation of Matson and Clapp, 1909) of the Florida Panhandle. His description of *S. floridanus* was based on two specimens. The holotype, taken from Harvey Creek in Leon County, is a young, thin-lipped adult (see plate 2, figures 1a and 1b), and the paratype, from Jackson Bluff some ten

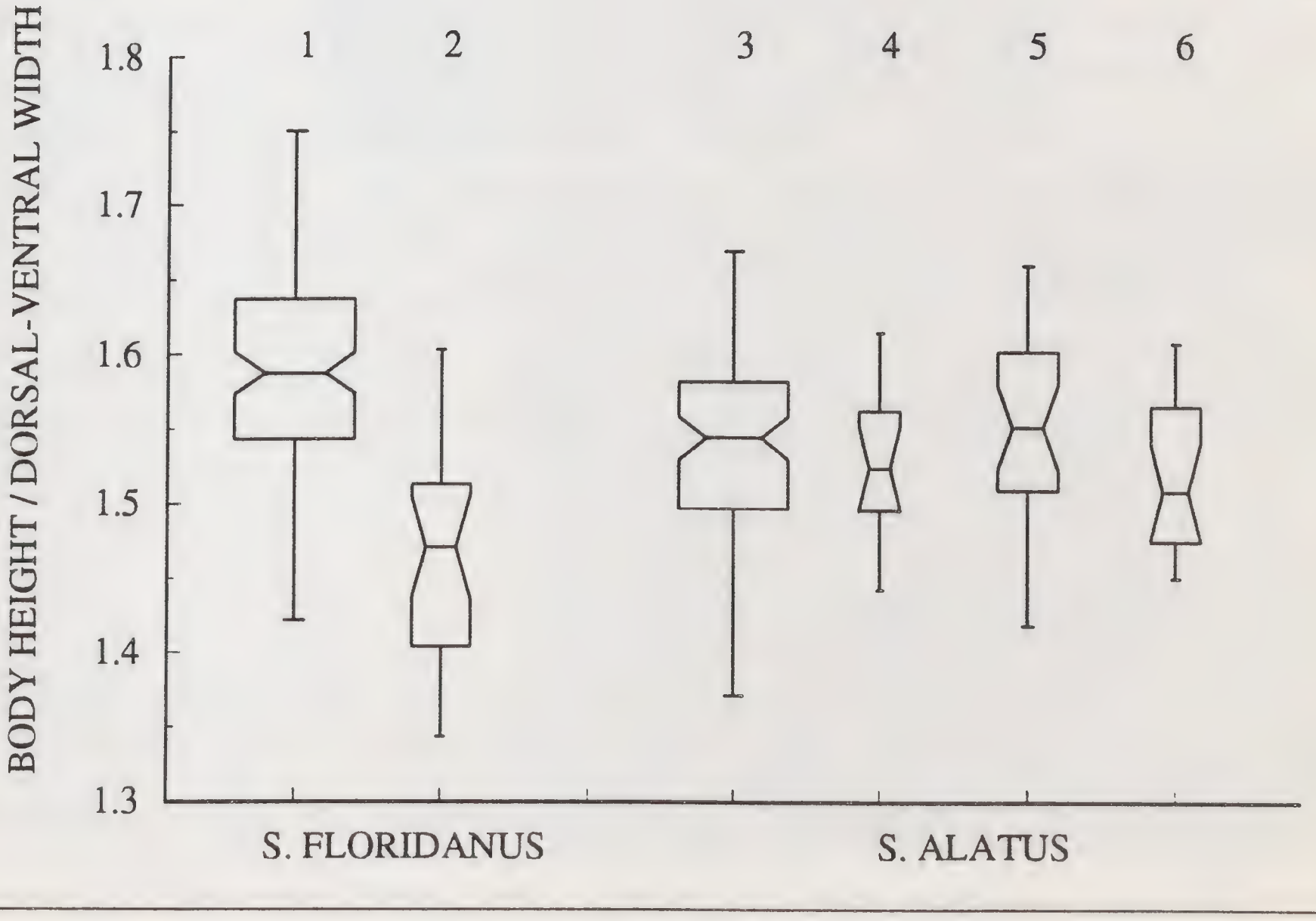


Text-figure 4. Notched box plots comparing [A] shell heights, [B] the fraction of total shell height subsumed by the body whorl, and [C] the ratio of height to dorsal-ventral width of the body whorl among samples of adult *S. floridanus* and *S. alatus.* For these, and all other box plots included in this study, the boxes inclose data for the middle 50% of the specimens in the sample, with the horizontal line indicating the median value for that sample. The width of each box is proportional to the square root of the sample size and the notches approximate the 95% confidence interval for the sample median. Vertical lines usually indicate the range of the data within the sample. However, individuals lying more than two times the height of the box beyond either end of the box are considered to be outliers, their positions being marked by a +. The sample locations and sizes are as follows: [1] lower Pinecrest beds (N = 107); [2] Jackson Bluff Formation (N = 34); [3] Campeche Coast (N = 87); [4] Florida Keys (N = 13); [5] Southwest Florida (N = 26); and [6] St. Andrews Bay (N = 19).

B


1
2
3
4
5
6
0.78
0.76
0.74
0.72
0.70
0.68
0.66
0.64
0.62
BODY HEIGHT / SHELL HEIGHT
S. FLORIDANUS
S. ALATUS

C


1
2
3
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5
6
1.8
1.7
1.6
1.5
1.4
1.3
BODY HEIGHT / DORSAL-VENTRAL WIDTH
S. FLORIDANUS
S. ALATUS

kilometers to the west, is a juvenile. Also available to Mansfield in the collections of the U. S. National Museum of Natural History were an adult specimen from Jackson Bluff with the spire tip missing and some fragmentary specimens from Harvey Creek.

Given the small sample size that Mansfield was working with, it is legitimate to consider the utility of each of the four distinguishing characteristics explicitly mentioned in his description for differentiating *S. floridanus* and *S. alatus*. To assess morphological variation over the range of *S. alatus*, the specimens taken from the five localities discussed above were analyzed and plotted separately. The *S. alatus* growth profile ultimately used to represent the species is based upon 73 juvenile and adult specimens taken from localities along the west coast of Florida from Naples in the south to St. Andrews Bay in the north. The growth profile of *S. floridanus* is based on a sample of 75 juvenile and adult specimens taken from the lower units of the APAC pit and nearby Quality Aggregates operation in northern Sarasota County, with a secondary sample of 69 juvenile and adult specimens of *S. floridanus* from the Jackson Bluff Formation analyzed for comparative purposes. It cannot be assumed that these two samples of *S. floridanus* were contemporary in the sense that the samples of *S. alatus* are. Indeed, based on studies of planktonic foraminifera, Akers (1979, p. 6) considers the *Strombus*-containing *Cancellaria* zone of the Jackson Bluff Formation to be slightly younger than the Pinecrest beds of southern Florida.[8])

Features Associated with Adult Shell Shape. Text-figure 4 provides a series of notched box plots summarizing some of the adult morphological features of *S. floridanus* and *S. alatus* Text-figure 4-A provides a comparative picture of adult shell heights. Text-figure 4-B represents one way to compare relative spire heights among taxa, portraying the fraction of total shell height taken up by the body whorl. Text-figure 4-C compares the ratio of shell height to shell width. The height and dorsal-ventral width of the body whorl were utilized for this ratio rather than shell height and maximum shell width so as to separate variations in relative spire height and the expansiveness of the adult lip, which tend to color estimates of shell "fatness," from consideration of the relative girth of the body whorl.

Several points are apparent in these plots. First, at least for the larger samples, there is considerable variation in these three statistics within each sample. Second, there is statistically significant morphological variation among the four samples of *S. alatus* for two of the three statistics.[9] Third, there is a similar degree of variation present in the two samples of *S. floridanus*. Fourth, there is extensive overlap in the ranges of each of the three statistics for *S. floridanus* and *S. alatus*. Thus, none of the three characteristics plotted can serve to identify individual specimens of *Strombus* with either taxon.

Mansfield's assertion that *S. floridanus* is shorter than *S. alatus* is certainly true on average for all of the material studied. From Text-figure 4-A it can be seen that the median shell height for the Pinecrest form of *S. floridanus* is almost 20 millimeters less than that for the nominate form of *S. alatus* from southwestern Florida, a reduction of almost 25%. However, the fact that the median values for shell height among the four samples of *S. alatus* them-

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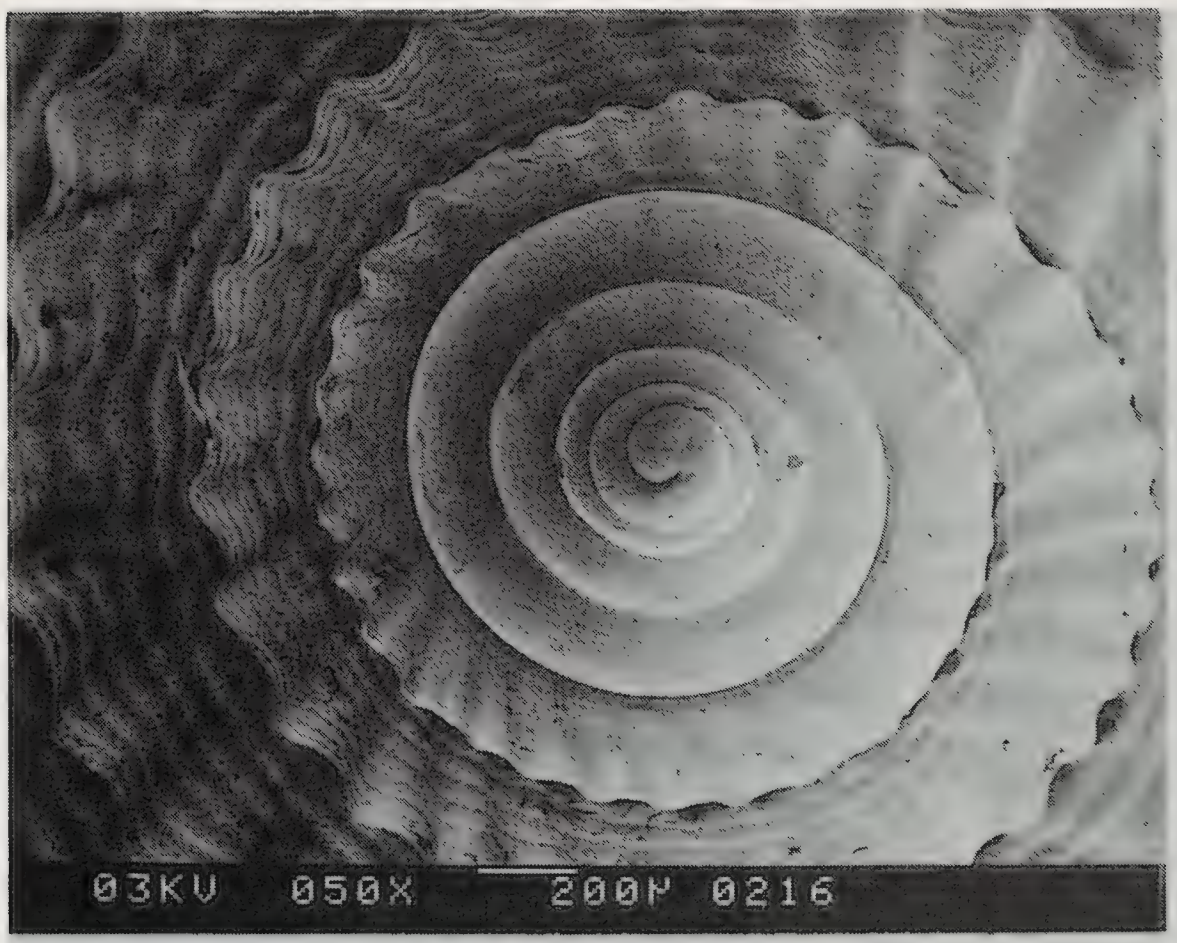
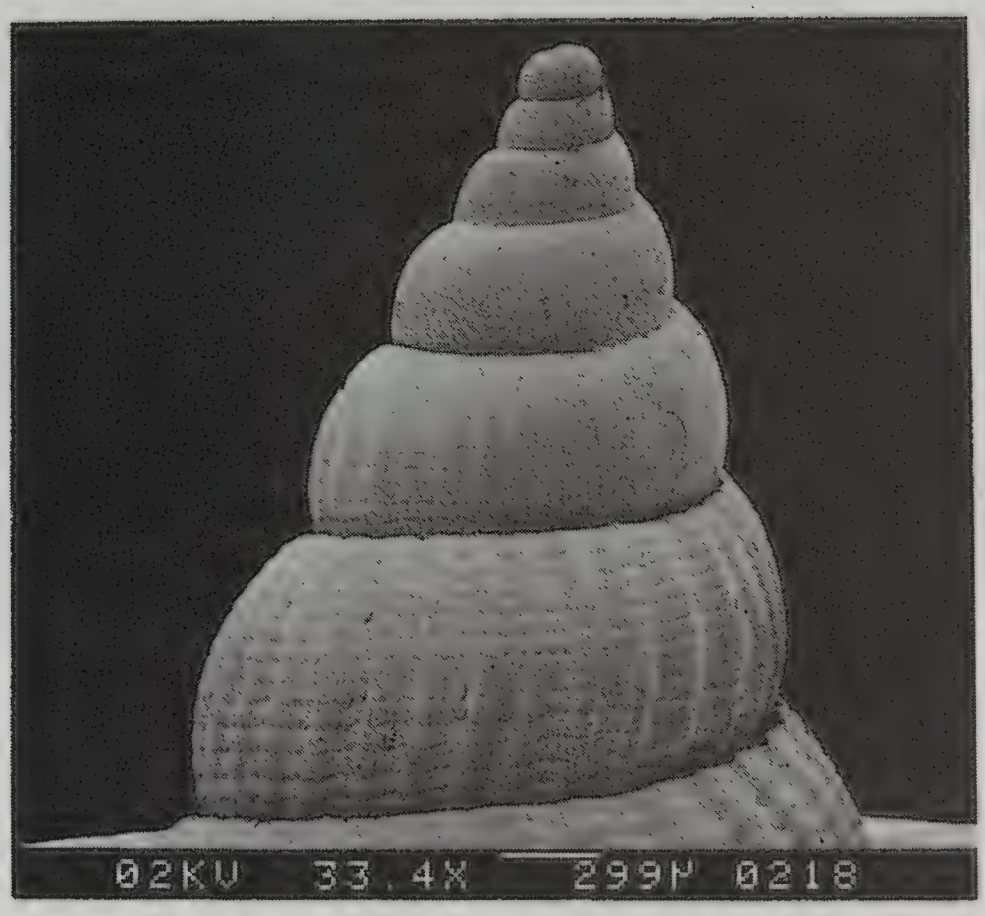
PLATE 1

Figure

1. *Strombus floridanus* Mansfield
   USNM 483764; height 12.1 mm, diameter 4.9 mm.
   Locality: Unit 7, APAC Pit, Sarasota, Florida (= TU 1000); lower Pinecrest beds.
   1a. SEM image. Apical view of the protoconch and initial whorls of the teleoconch; scale bar = .2 mm.
   1b. SEM . Side view of the protoconch and initial whorls of the teleoconch; scale bar = .3 mm.
   1c. SEM image. Closeup of whorl five showing more clearly the transition from protoconch to teleoconch; scale bar = .11 mm.



1a



1b

1c

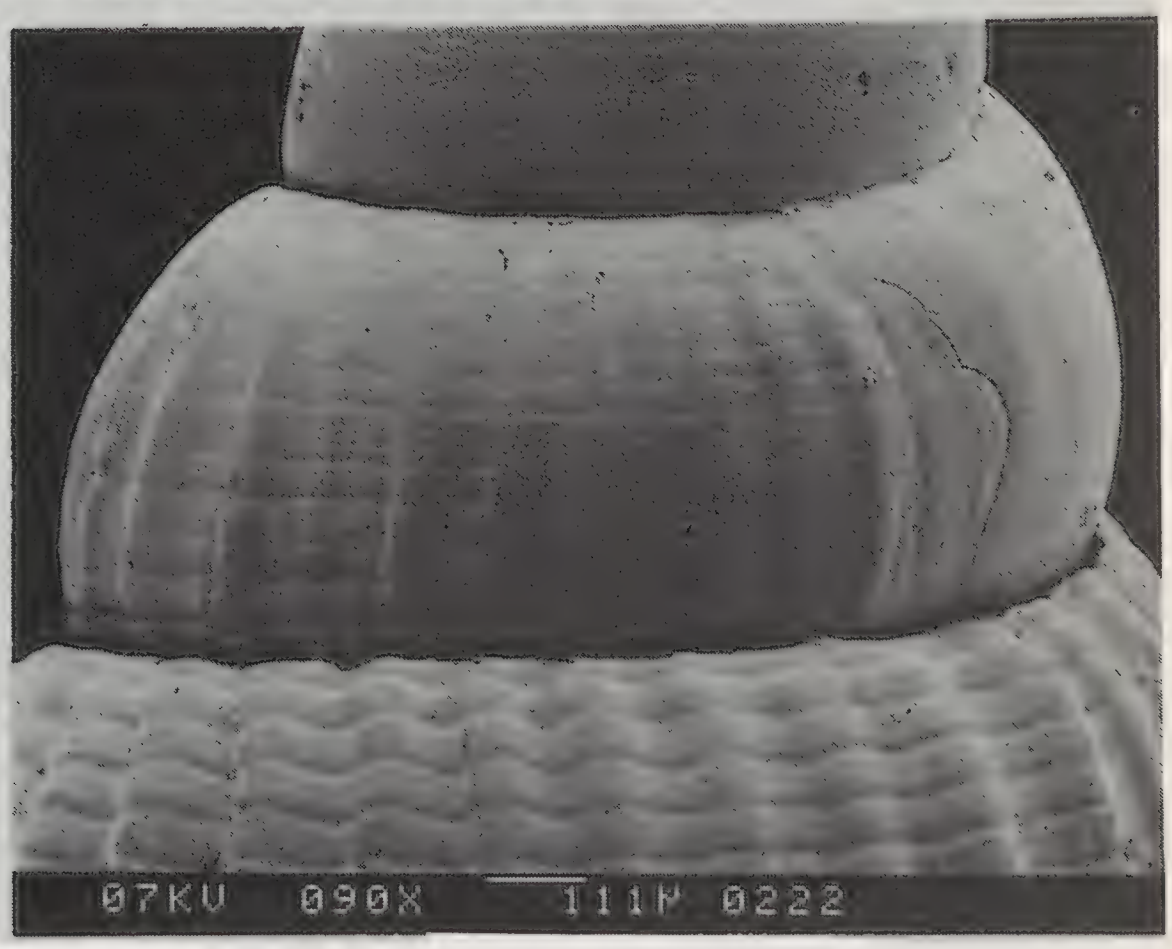


PLATE 1

selves differ by almost 20 millimeters should cause one to use extreme caution in proposing adult size as a taxonomically significant morphological characteristic among *Strombus*.

Text-figure 4-B does not substantiate the claim made by Mansfield that the Jackson Bluff form of *S. floridanus* has a proportionately shorter spire than *S. alatus*. Interestingly, the Pinecrest form of *S. floridanus*, unknown to Mansfield at the time, does have a slightly shorter (3%) spire than any known form of *S. alatus*. However, what is perceived as differences in relative spire height among *Strombus* specimens is usually rather a function of overall spire shape (*i.e.*, whether concave, convex or straight sided in aspect) and the comparative height and width dimensions of the shell. The spire of a "fat" specimen will appear to be shorter than that of a "thin" specimen of similar longitudinal dimensions because the spire angle will be greater. Also a markedly concave spire will appear to be shorter than a straight-sided or convex spire of similar longitudinal dimensions because it is inherently less substantial to the eye. It is these features that probably led Mansfield to make his claim about the relative spire heights of the two taxa. This can be seen clearly from Text-figure 4-C. The Jackson Bluff form of *S. floridanus* is markedly "fatter" than any form of *S. alatus* analyzed. The Pinecrest form of *S. floridanus*, on the other hand, is less rotund than its *S. alatus* counterparts. All of this suggests that relative spire height is a problematic and unreliable morphological characteristic for differentiating these taxa.

Axial and Spiral Ornamentation of Adult Specimens. Mansfield also refers to *S. floridanus* as having "fewer nodules or tubercles" than *S. alatus*. However, in the discussion of the taxon itself, it is clear that he is referring to the fact that, unlike Recent *S. alatus*, axial ornamentation in the form of shoulder knobs or blunt spines is absent from the body whorl. Indeed, of literally thousands of specimens of *S. floridanus* observed by the author, none have been found to have peripheral axial ornamentation on the body whorl.[10] As for *S. alatus*, Clench and Abbott (1941) and others have assumed that the smooth-shouldered specimen figured by Martini (1777, pl. 92, fig. 894) and utilized by Gmelin in naming the taxon represents a spineless Recent specimen from Floridian waters. If so, it is certainly an atypical specimen that was figured. Goodrich (1944) published a paper on variation within *S. alatus* based upon a sample of 1100 adult specimens collected on Sanibel Island over a period of two decades in the early twentieth century. Therein he noted that 923 specimens, or some 84% of the sample, had fully developed spinose or nodulous axial ornamentation on the body whorl. In the remaining 177 specimens, axial ornamentation was either mal-formed, reduced in extent to only a portion of the body whorl, or entirely absent from that final whorl. Unfortunately, separate statistics were not presented for these latter three categories. The author's own experience observing *S. alatus* on Sanibel Island during the past decade confirms the rarity of spineless specimens at the type locality. Also, no spineless Recent individuals have been found among several hundred *S. alatus* specimens studied from Campeche Coast of the Yucatan Peninsula. Hence, while there may be populations of *S. alatus* wherein the percentage of spineless individuals is higher, the evidence at hand suggests that this is an uncommon occurrence in the taxon.

The spiral sculpture on the body whorl, although described to some extent for the new taxon by Mansfield, was not referred to by him in differentiating that taxon from *S. alatus*. In both taxa the external spiral sculpture may be more or less strongly expressed in individual specimens and, when present, the form of the sculpture shows the same range of expression. The same can be said for the submarginate costae and columellar denticles found inside the aperture of adult specimens. It is with respect to the series of longer lirations or rugosities on the parietal wall within the aperture that *S. alatus* and *S. floridanus* differ most noticeably. Their presence is extremely rare in *S. alatus* but they appear in up to 20% of the specimens in samples of *S. floridanus*. Mansfield did not make use of this characteristic.

Adult Color Patterns. Mansfield noted on the body whorl of his adult specimens the

presence of "angled colored bands" having their apices pointed backwards (*i.e.*, away from the lip) and aligned along the midpoint of the body whorl. The pattern created by these bands most often consists of a parallel series of dark chevrons one or two millimeters across and separated by slightly wider interstices (see Text-figure 5). Although nothing quite like it exists among *Strombus* sensu stricto today, this chevron pattern seems to have been a fairly common characteristic among the Caribbean *Strombus* of the Pliocene and Pleistocene. It seems to be almost ubiquitous among adult *Strombus pugiloides* Guppy, 1873, in the Bowden Formation of Jamaica. It is also common among adults of an unnamed subspecies or form of *S. pugiloides* found in the Rio Banano Formation of Costa Rica, and has been seen under UV illumination in at least one specimen of a form of *Strombus gatunensis* Toula, 1909. The persistence of color pattern in fossils appears to be strongly influenced by the conditions of preservation, making it difficult to determine how common patterning was in a taxon such as *S. floridanus*. Most Pinecrest *Strombus* specimens in collections do not show any pattern even under UV illumination. However, the author has twice come upon recently uncovered pockets of *S. floridanus* in phase 6 of the Quality Aggregates operation wherein virtually every adult specimen retained some remnant of the chevron pattern, suggesting that it was a common if not universal feature.[11]

Goodrich (1944) recorded 68 specimens from the lot of 1100 *S. alatus* analyzed as having an irregular "mottling" over nearly the entire surface of the body whorl and another 83 as exhibiting a more regular zigzag pattern (see plate 4, figure 2). While the presence of "regular" patterning in about 8% of a sample may seem to be of little diagnostic value, when compared with the other two extant species of *Strombus* sensu stricto, it is significant. Patterning has never been recorded in *S. gracilior* and has been witnessed by this investigator only once in *S. pugilis*, as a vestigial patch of pattern on the ventral shoulder of the body whorl just in front of the aperture.

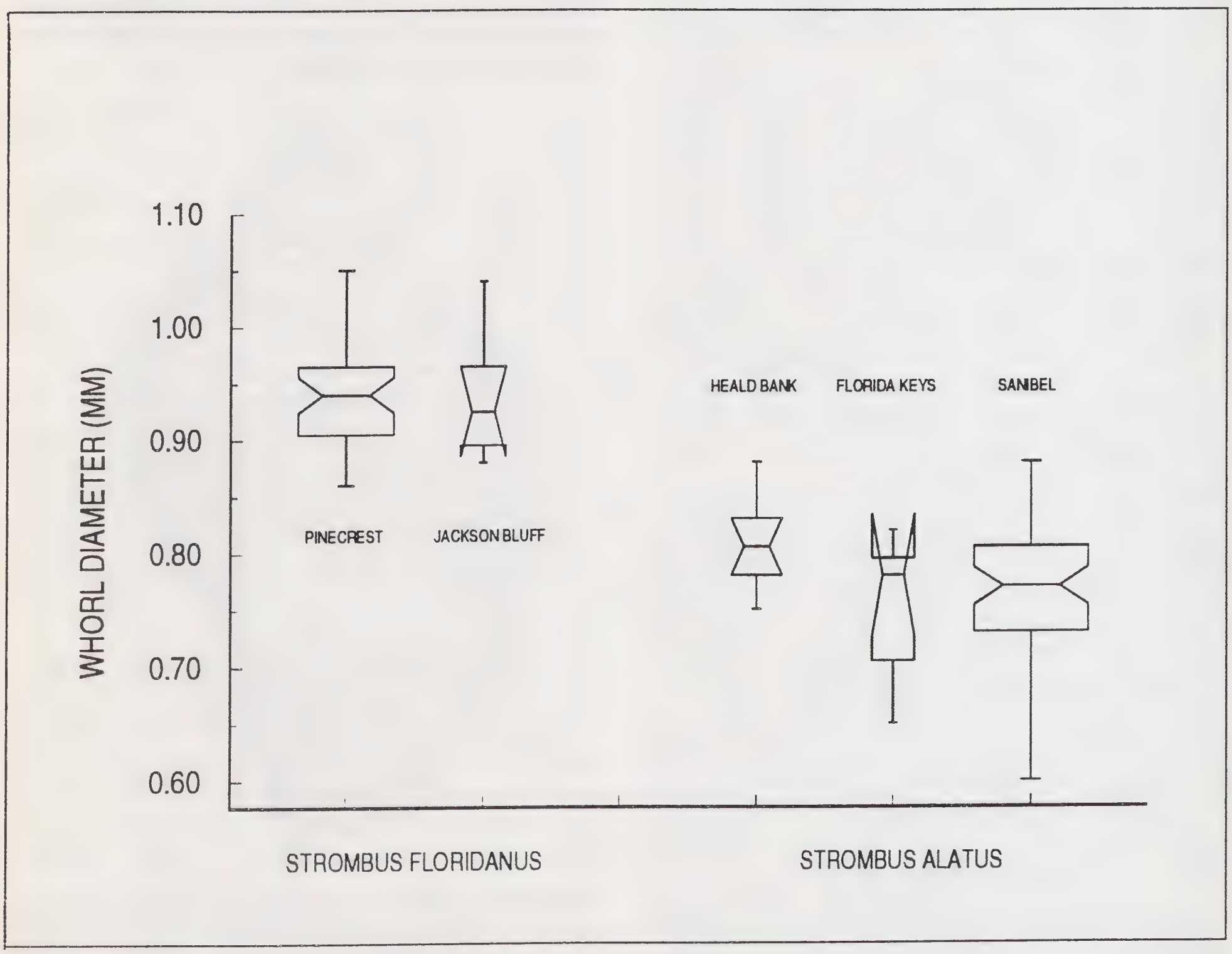
In summary, normal approaches to the study of shell morphology involving adult size, shape, sculptural ornamentation, and color patterning, provide no diagnostic features that can be used unequivocally to separate *S. floridanus* from *S. alatus*. When large samples of both taxa are analyzed one is left only with tendencies, some of which yield statistically significant differences. Adult *S. alatus* tend to be larger in size, to have axial sculpture that persists onto the body whorl in the form of shoulder knobs or spines, to be less likely to exhibit parietal rugosities, and to be less likely to have distinct axial color markings on the body whorl. Other features such as relative spire height and shell "fatness" seem to provide no insight at all. Hence, although the tendencies suggest very strongly a phylogenetic relationship between the two forms, it still might not be possible to determine the identity of individual specimens based upon such information. Can an ontogenetic analysis provide additional insights into the differences between these two taxa?

Text-figure 5. Depiction of the distinctive chevron color pattern often visible under long wave ultra-violet illumination (3660 Å). Although the specimen portrayed represents Taxon C, this pattern is reasonably common on specimens of *S. floridanus* and Taxon B as well.

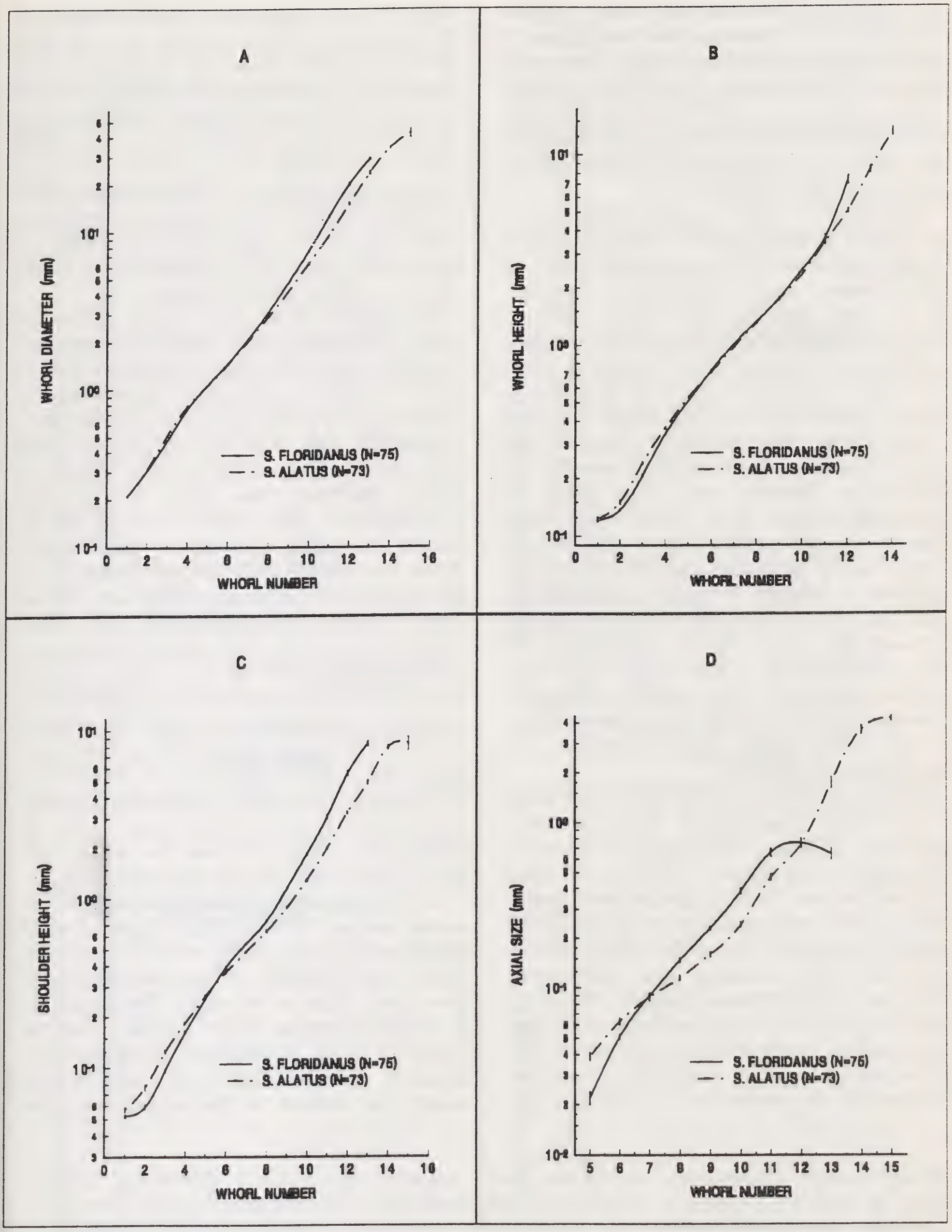
Ontogenetic Analysis. One important aspect of shell development clearly related to the ontogeny of the animal within is the transformation from protoconch to teleoconch, delineated by that point in the shell development of *Strombus* at which axial and/or spiral ornamentation is initiated. Unlike certain other gastropod families, this point of transition is not marked by an easily discernable varix. Nor is the initial ornamentation strongly expressed (see plate 1). The initial axials are usually microscopically fine and may continue that way for as much as a quarter of a whorl. Spiral sculpture tends to be most strongly expressed initially at and below the periphery of the whorl where it will be hidden by subsequent whorls.

The results of a careful microscopic analysis of well-preserved juvenile specimens are presented in Text-figure 6. While some of the sample sizes are too small to permit an assessment of intraspecific variability, it is clear that the two taxa themselves differ from one another. There is a decline in the median terminal diameter of the protoconch from 90-95 mm in *S. floridanus* to 75-80 mm in *S. alatus*, with almost no overlap in the ranges of those diameters for the two taxa. This reduction is driven primarily by a reduction in the number of whorls in the protoconch from a mean of 4.6 in the lower Pinecrest form of *S. floridanus* to 3.9 in the nominate form of *S. alatus*. However, while protoconch size does represent a good diagnostic feature for differentiating these two taxa, it tends to be a feature of limited usefulness since the early spire whorls are seldom retained in adult specimens.

Growth profiles for these two taxa (Text-figures 7 to 11) suggest a suite of other



Text-figure 6. Notched box plot comparing whorl diameters at the end of the protoconch among samples of *S. floridanus* and *S. alatus*. The sample sizes are as follows: lower Pinecrest beds (N = 36); Jackson Bluff Formation (N = 8); Heald Bank (N = 10); Florida Keys (N = 8); and Sanibel Island (N = 51).



Text-figure 7. Comparison of the primary growth characteristics for *S. floridanus* and *S. alatus*. [A] compares the growth in whorl diameter, [B] the growth in whorl height, [C] the growth in shoulder height, and [D] the growth in axial element size. The curves connect the mean values of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values.

developmental differences that persist throughout shell ontogeny. Text-figures 7 and 8 compare profiles for the Pinecrest form of *S. floridanus* and for *S. alatus* found along the Gulf Coast of Florida. Text-figures 9, 10 and 11 provide insights into the nature and extent of intraspecific developmental variation.

Text-figure 7 shows a recurring pattern in the four primary growth characteristics. During protoconch development and, in some cases, early teleoconch development, the curves are lower for *S. floridanus* than for *S. alatus*. For later teleoconch development the reverse is true. For this to occur, the growth **rates** for *S. alatus*, except for the early stages of larval development, must be lower than the corresponding (*i.e.*, same whorl) rates for *S. floridanus*. Hence, not only does *S. floridanus* mature at a smaller size, but it does so in fewer whorls than would be predicted based upon the growth rates exhibited by *S. alatus*. It is also important to note that the differentials in growth rates between taxa vary from measure to measure. Changes in whorl height are very similar over much of the growth of the teleoconch. Shoulder heights and axial size, on the other hand, show marked dissimilarities throughout.

The four comparative second order plots of Text-figure 8 provide an idea of the consequences of these differing growth rates. Looking at Text-figure 8-A it can be seen that each curve yields a protoconch maximum, a teleoconch maximum and an intervening minimum. The salient differences are that both maxima are more pronounced in *S. floridanus* but the minimum occurs later. For each taxon the minimum comes about 1.5 whorls after the end of the protoconch, the shift mirroring nicely the differences in protoconch size already noted. The plot indicates that the spire of *S. floridanus* shows a more marked tendency towards convexity during the late protoconch and early teleoconch, followed by a relatively greater tendency towards concavity in later stages of growth. The former is difficult to see except under a microscope (see plate 1) whereas the latter is clearly visible to the naked eye and is, at least in part, the reason that Mansfield perceived the spire of *S. floridanus* as being "shorter" than that of *S. alatus*.

Text-figure 8-B also shows for each curve protoconch and teleoconch maxima flanking an intermediate minimum that is located at the same points in overall development as in the previous plot, thereby suggesting that it is the decreasing and subsequent increasing growth rates in whorl diameter that give rise to this phenomenon. The maxima are in this instance curiously bimodal, particularly those associated with the development of the teleoconch. Also significant are the relative heights of the protoconch and teleoconch maxima for each taxon. In the case of *S. floridanus* the protoconch maximum is considerably higher than that for the teleoconch, providing an overall downward trend to the curve. For *S. alatus* the opposite is true. This results, for *S. floridanus*, in a spire wherein the whorls appear to be progressively more sloping and, for *S. alatus*, in a spire wherein the whorls appear to be progressively more tabulate.

In Text-figure 8-C the important differences are in the average slope of each curve over the first eight whorls and in the extent and rapidity of the upward turn of the curves after whorl eight. The curve for *S. alatus* suggests whorl profiles that remain turreted throughout ontogeny, the situation ameliorated only slightly for about four whorls of the teleoconch. The

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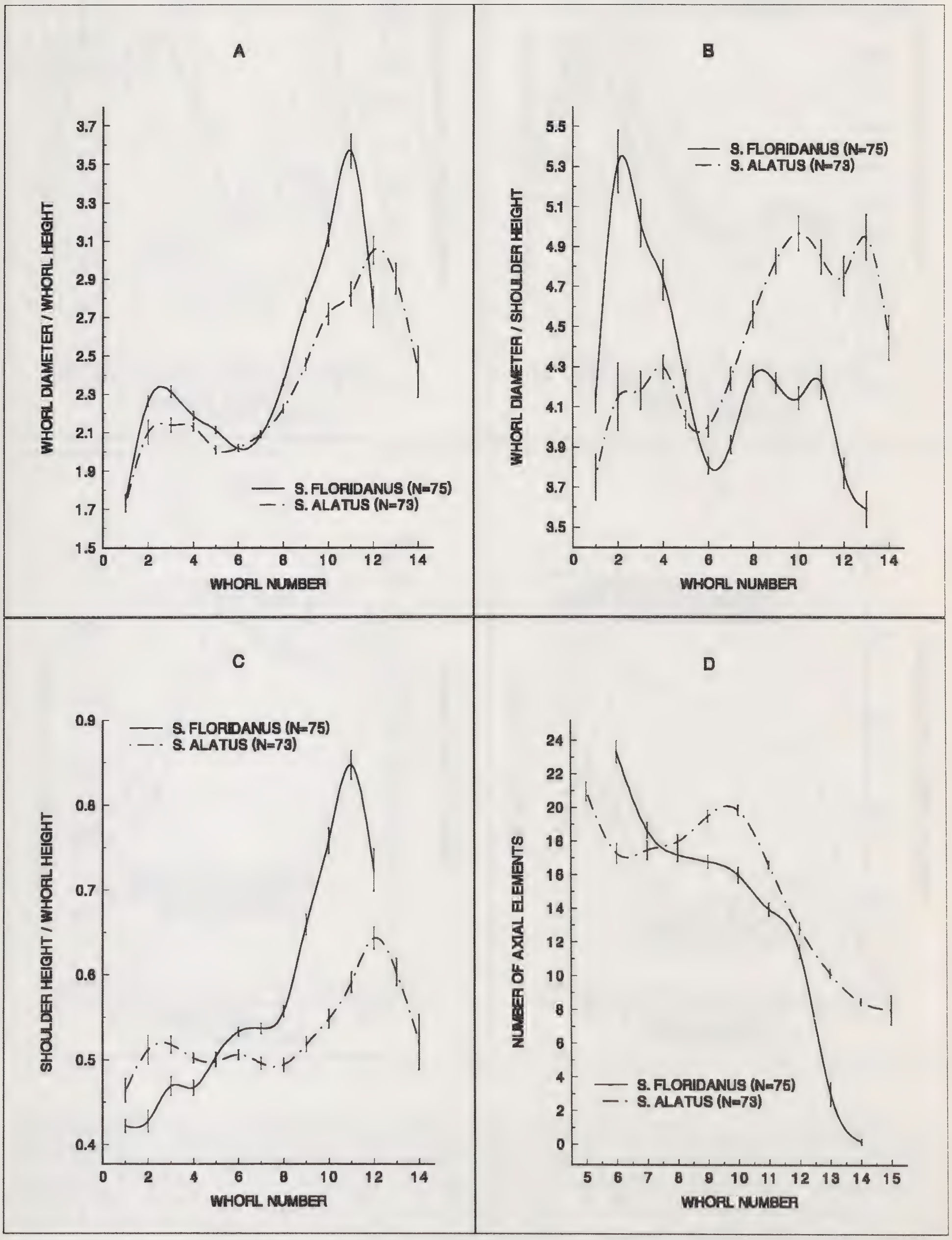
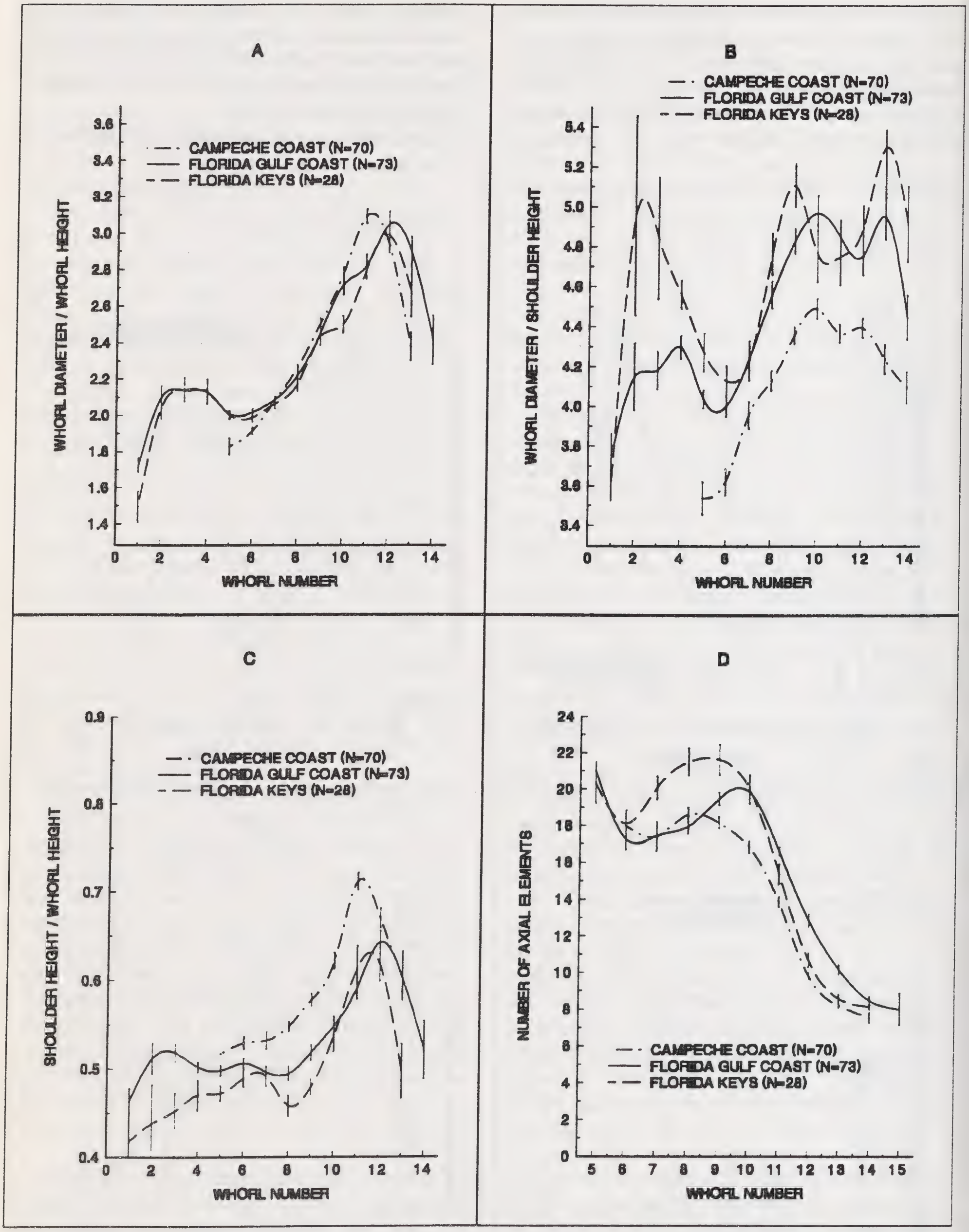
Text-figure 8. Comparison of second order growth curves for *S. floridanus* and *S. alatus*. As with Text-figure 2, [A] conveys information concerning whether the spire profile is seen as concave, convex, or straight sided, [B] conveys information as to whether individual whorl profiles appear to be tabulate or sloping, [C] conveys information concerning the placement of the suture of the succeeding whorl relative to the whorl periphery and, hence, whether a whorl appears to be turreted or embedded, and [D] portrays changes in the number of axial elements per whorl (including resting varices) over shell development. The curves connect the mean values of ratios of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values. >

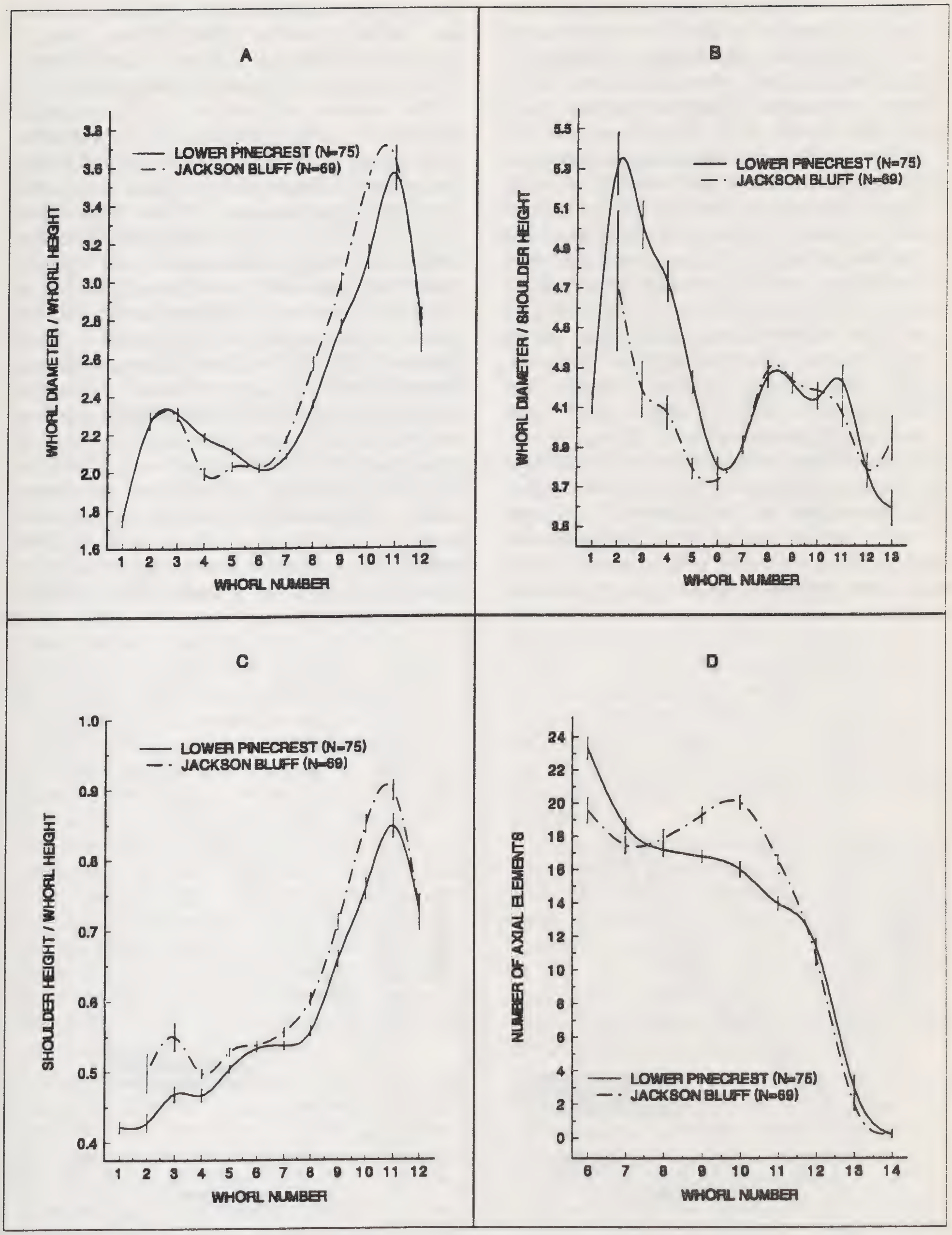
curve for *S. floridanus* suggests whorl profiles that become progressively less turreted, slowly at first and then rapidly and almost completely, culminating in a whorl wherein the peripheral axial elements are almost overrun by the suture of the succeeding whorl just prior to adulthood. It is this dual tendency towards more sloping, less turreted whorl profiles in *S. floridanus* that Mansfield referred to in his comparison of the spire outlines.

The earlier onset of axial expression in





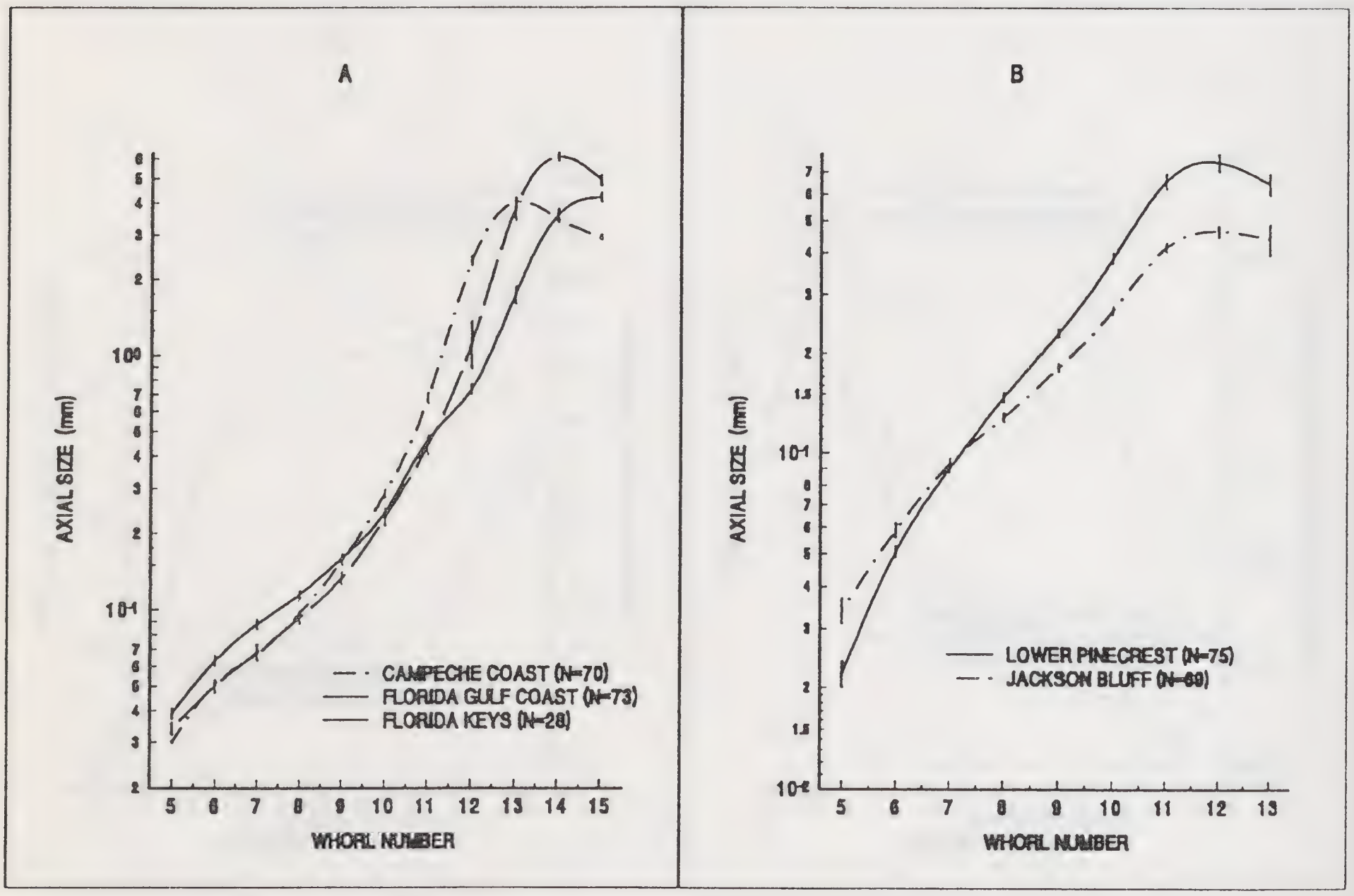
Text-figure 9. Comparison of second order growth curves for three *S. alatus* samples from different localities over the range of that taxon. [A] through [D] represent the same features as in Text-figure 8. The curves connect the mean values of ratios of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values.



Text-figure 10. Comparison of second order growth curves for two samples of *S. floridanus* from different Pliocene formations, the lower Pinecrest beds of southern Florida and the Jackson Bluff Formation of the Florida Panhandle. [A] through [D] represent the same features as in Text-figures 8 and 9. The curves connect the mean values of ratios of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values.

Text-figure 8-D for *S. alatus* is a direct result of the smaller size of the protoconch, while the significantly higher endpoint reflects the fact that most specimens of *S. alatus* retain axial elements on the body whorl but those of *S. floridanus* do not. The intervening minimum and maximum in the *S. alatus* curve that are not reflected in the *S. floridanus* curve must be understood in terms of the complex interplay between the growth of axial element size during ontogeny and the growth in whorl diameter and, hence, circumference. If element size is increasing faster than whorl circumference, the number of elements capable of being placed along the periphery of a whorl must decline. Conversely, if circumference is increasing faster than element size, then more elements can be accommodated on a whorl. Referring once again to Text-figure 7-D, it can be seen that the rate of growth of axial elements in *S. floridanus* remains fairly constant from whorl seven to whorl eleven. For *S. alatus*, on the other hand, the rates are initially lower than those for *S. floridanus* but they increase continuously from whorl seven through whorl twelve.

The nature and extent of intraspecific variation can best be seen by comparing second order growth curves. The Florida Keys and Campeche samples are compared to the nominate Florida Gulf Coast form of *S. alatus* in Text-figure 9. What appear as small differences in primary growth values and rates result in rather obvious differences in these second order curves. This is particularly true for Text-figures 9-B an 9-C wherein comparatively larger shoulder height values for Campeche specimens yield substantially shifted second order plots, and slightly altered protoconch whorl diameter and shoulder height values for Florida Keys specimens yield substantially altered protoconch maxima. However, a closer look at this suite of curves also demonstrates similar overall patterns of growth (*i.e.*, similar



Text-figure 11. Comparison of the growth in axial element size among [A] three *S. alatus* samples from different localities over the range of that taxon, and [B] two samples of *S. floridanus* from different Pliocene formations, the lower Pinecrest beds of southern Florida and the Jackson Bluff Formation of the Florida Panhandle. The curves connect the mean values of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values.

placements of and relationships among maxima, minima, and inflection points) for the different samples, suggesting that the plots may indeed be useful taxonomic indicators.

Modest differences in the values and rates for the primary growth elements in *S. floridanus* also result in clearly discernable differences in the second order growth curves (Text-figure 10). In this case, distinctly different protoconch profiles can be seen in each of the first three plots. Even though overall sample sizes may be large (75 in this case for the Pinecrest material and 69 for the Jackson Bluff material); however, individual specimens seldom if ever yield information for each and every whorl in the growth profile. Adult specimens have never been found to contain a complete, uneroded protoconch. Except for those just arriving at adulthood, it is unlikely that an adult specimen will retain any useful information concerning protoconch development. And juveniles, for their part, do not contain information about those growth characteristics immediately preceding adulthood. Hence, the profiles tend to be most reliable for the middle whorls of development, with the reliability of the protoconch profile being directly related to the number of well-preserved juvenile specimens present in the sample. In the example under discussion, the number of well-preserved juvenile specimens in the Pinecrest sample was considerably larger (39) than that for the Jackson Bluff sample (9). Again, the important point with respect to the two profiles presented in Text-figure 10 is that they show similar patterns of growth, patterns that differ from those present in Text-figure 9 for samples of *S. alatus*.

Intraspecific differences can also be seen with respect to the growth of axial element size. Text-figure 11-A compares axial growth profiles for both the Campeche and Florida Keys samples with the Florida Gulf Coast material utilized in constructing the basic *S. alatus* profile. The samples from the more southerly portions of the species' range have rather similar profiles with somewhat lower initial values than those found in the nominate form, more rapid rates of growth over whorls eight, nine and ten, and terminal "tails" suggesting that the largest axial elements on the penultimate whorl tend to be somewhat larger than those on the body whorl. The entire suite of growth rates for the Jackson Bluff sample is less than the corresponding rates for the Pinecrest sample (Text-figure 11-B). Yet, when Text-figure 11-B is compared directly with Text-figure 11-A, it can be seen that each taxon again has a typical pattern of development. In the case of *S. floridanus*, growth rates remain fairly constant from the end of whorl seven through whorl eleven, whereas, for *S. alatus*, the growth rates increase markedly and persistently over the same whorls. Taking into account all of the data plotted in Text-figures 9, 10 and 11, it is clear that samples of *S. floridanus* and *S. alatus* yield two reasonably consistent families of growth profiles, each representing, at least to some extent, the nature and extent of developmental variation within that taxon.

In summary, *S. floridanus* and *S. alatus* differ not only in adult morphological characteristics involving size, shape, ornamentation and color pattern, but also in ontogeny as well. Although the final product is inherently easier to study than the process, an understanding of the process can shed important light on the final product, particularly on that aspect of the product (the spire) that is an historical record of the process.

If one assumes not only that *S. alatus* differs from *S. floridanus* but that it represents the Recent descendent of that Pliocene species, then Text-figure 6 implies that there has been about a 15% reduction in the size of the protoconch during the past three million years in this lineage, while Text-figures 7 and 8 suggest an additional suite of developmental changes:

- in Text-figure 8-A a reduction in both the protoconch and teleoconch maxima, corresponding to spire forms that are decreasingly concave in overall aspect;
- in Text-figure 8-B a transformation in the shape of the plot from one of overall decline, corresponding to a spire profile with successively more sloping whorl shoulders, to one of overall increase, corresponding to a spire profile with successively more tabulate whorls;
- in Text-figure 8-C a flattening of the plot over the whorls of the protoconch and early teleoconch, together with a gradual

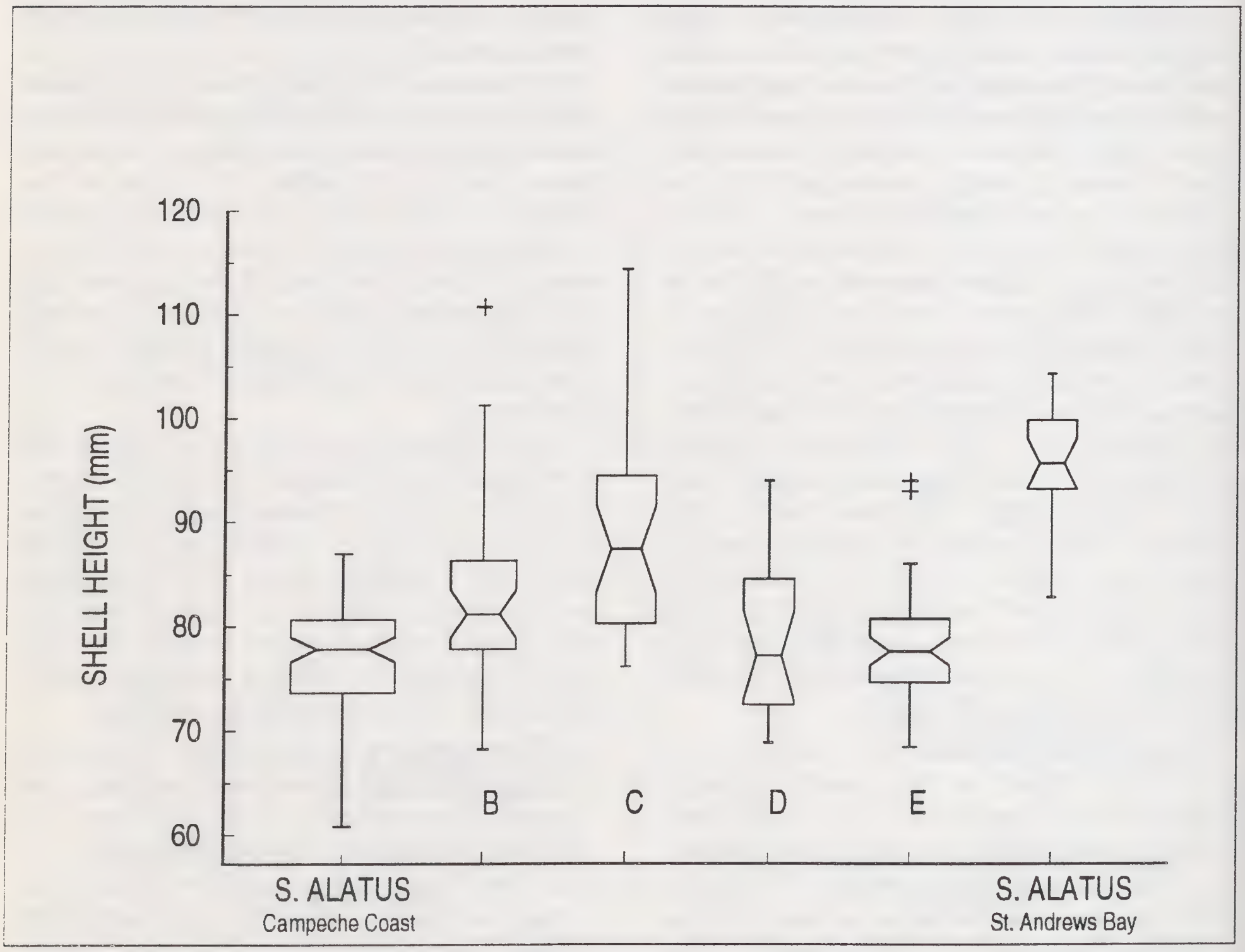
reduction of the teleoconch maximum, signifying a shift towards a more turreted spire outline;

- in Text-figure 7-D a transformation from fixed to increasing growth rates for axial ornamentation over the middle teleoconch whorls, together with an increase in the maximum value of element size.

One can postulate two hypotheses with respect to this process of morphologic change. The first assumes a series of incremental changes unfolding over all or much of the time interval. The second assumes a single shift from one morphological state to the other at some particular moment in time. This second hypothesis, in turn, offers two alternative possibilities. The first of these postulates that all of the morphological features outlined above are "coupled" and, therefore, go through the shift at the same point in time (*i.e.*, that all intervening fossil forms can be identified either with *S. floridanus* or *S. alatus*). The second postulates that some or all of the morphological features analyzed above are "decoupled" allowing the shifts in those particular features to take place at different geological times. Such decoupled changes in morphologic features would suggest that at least some of the intervening forms should be considered to be distinct chronospecies.

Analysis of Intervening Forms.

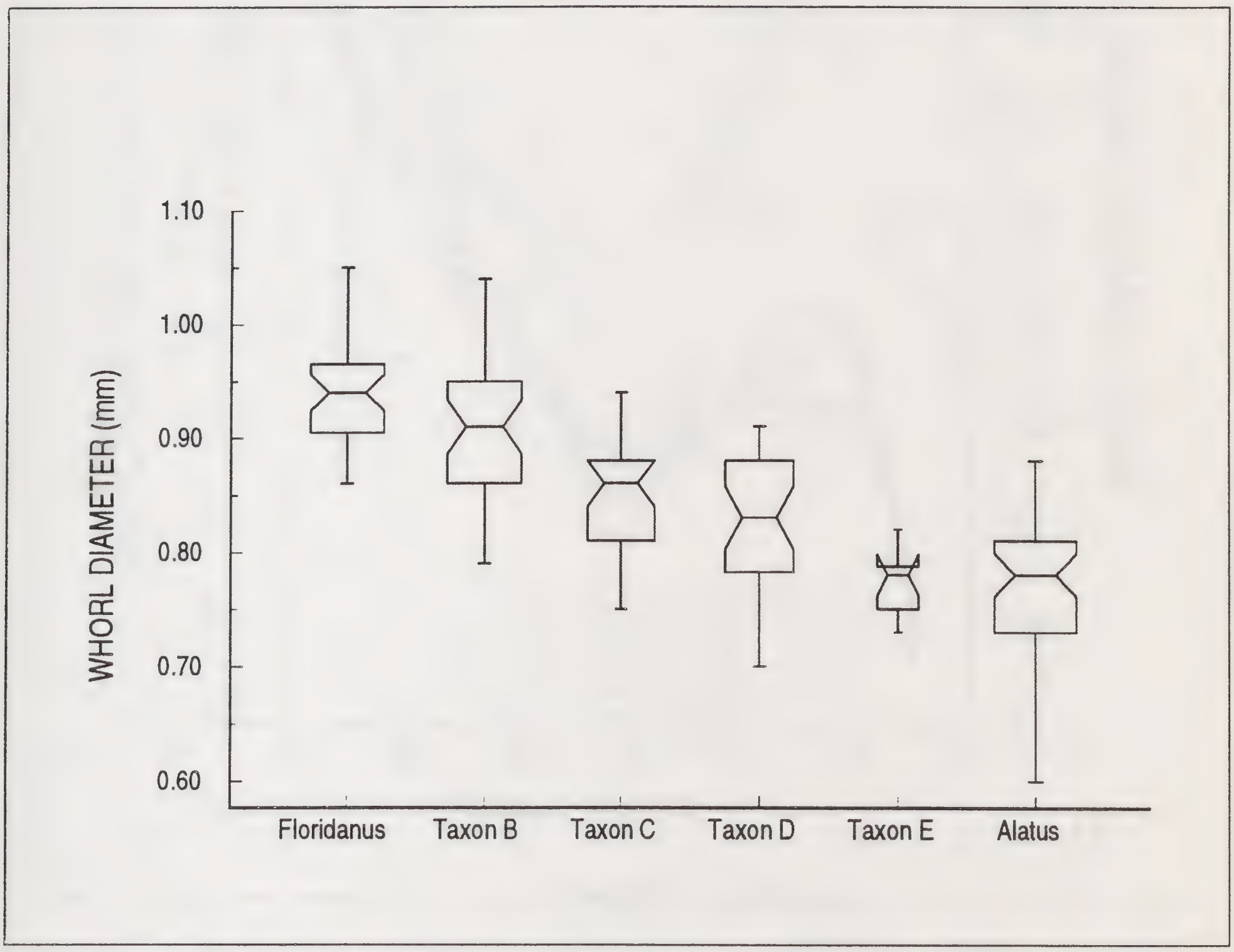
In the rich fossil record of southern Florida *S. floridanus* is present only in the lower part of the Pinecrest beds. Sub-



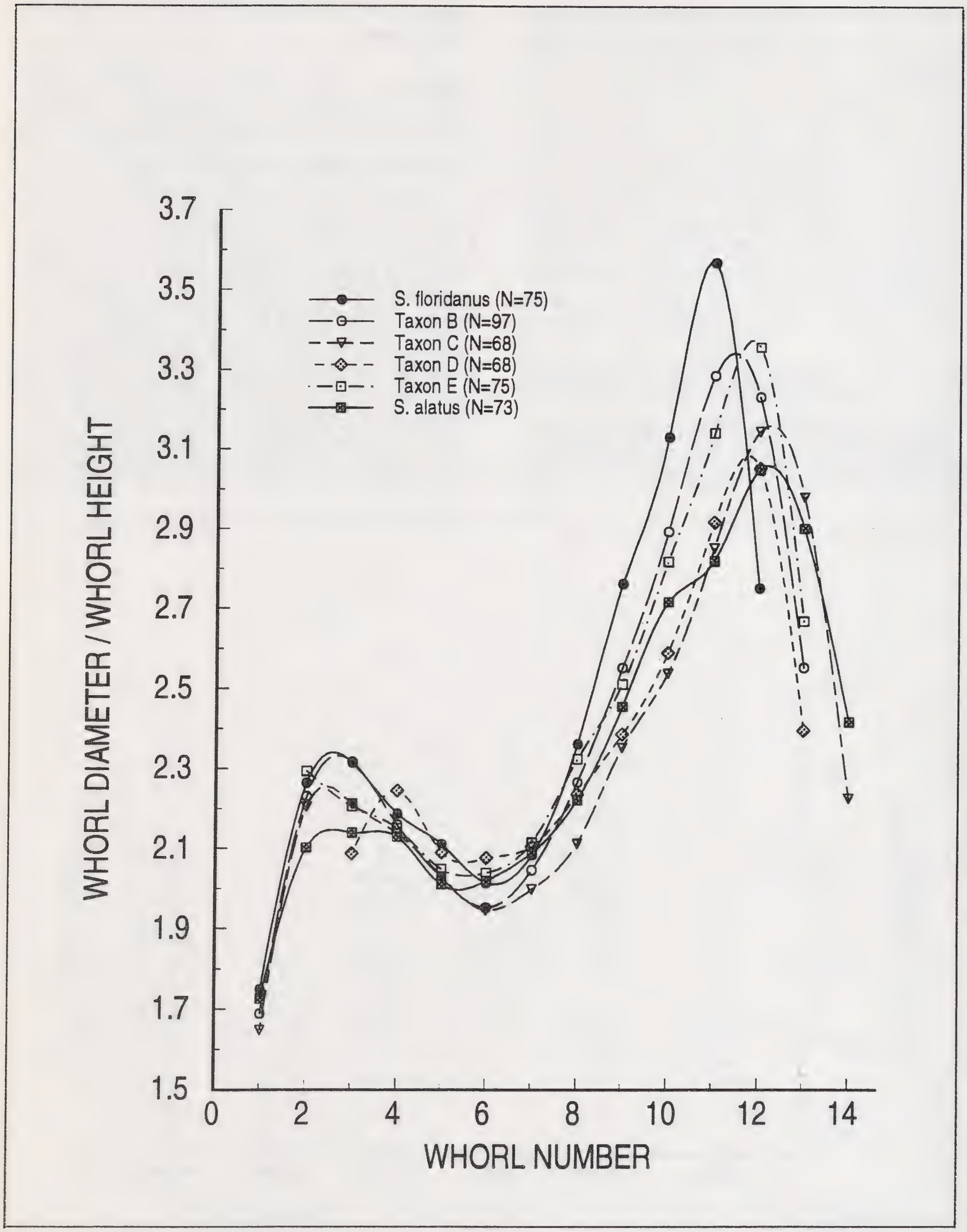
Text-figure 12. Notched box plot comparing shell heights among samples of various adult fossil *Strombus*. The fossil forms included and their sample sizes are as follows: Taxon B, upper Pinecrest beds (N = 34); Taxon C, Caloosahatchee Formation (N = 28); Taxon D, Bermont Formation (N = 20); and Taxon E, post-Bermont units (N = 50). The *S. alatus* samples with the largest (St. Andrews Bay) and smallest (Campeche Coast) median shell heights have been reintroduced from Text-figure 4-A for comparison.

sequent stratigraphic horizons contain a series of closely allied forms of *Strombus* sensu stricto that can be utilized to test the competing hypotheses set forth above. Horizons included herein for this purpose are: (1) the upper Pinecrest beds (corresponding to units 2-4 of Petuch at the APAC pit); (2) the Caloosahatchee Formation; (3) the Bermont Formation; and (4) post-Bermont units (usually referred to either the Fort Thompson or Coffee Mill Hammock Formations). The forms associated with these horizons are provisionally referred to as Taxon B, Taxon C, Taxon D and Taxon E, respectively. By determining which of the hypotheses concerning the nature of morphologic change is supported by the data from these intervening forms it should be possible to determine how many of these forms deserve to be considered as distinct taxa.

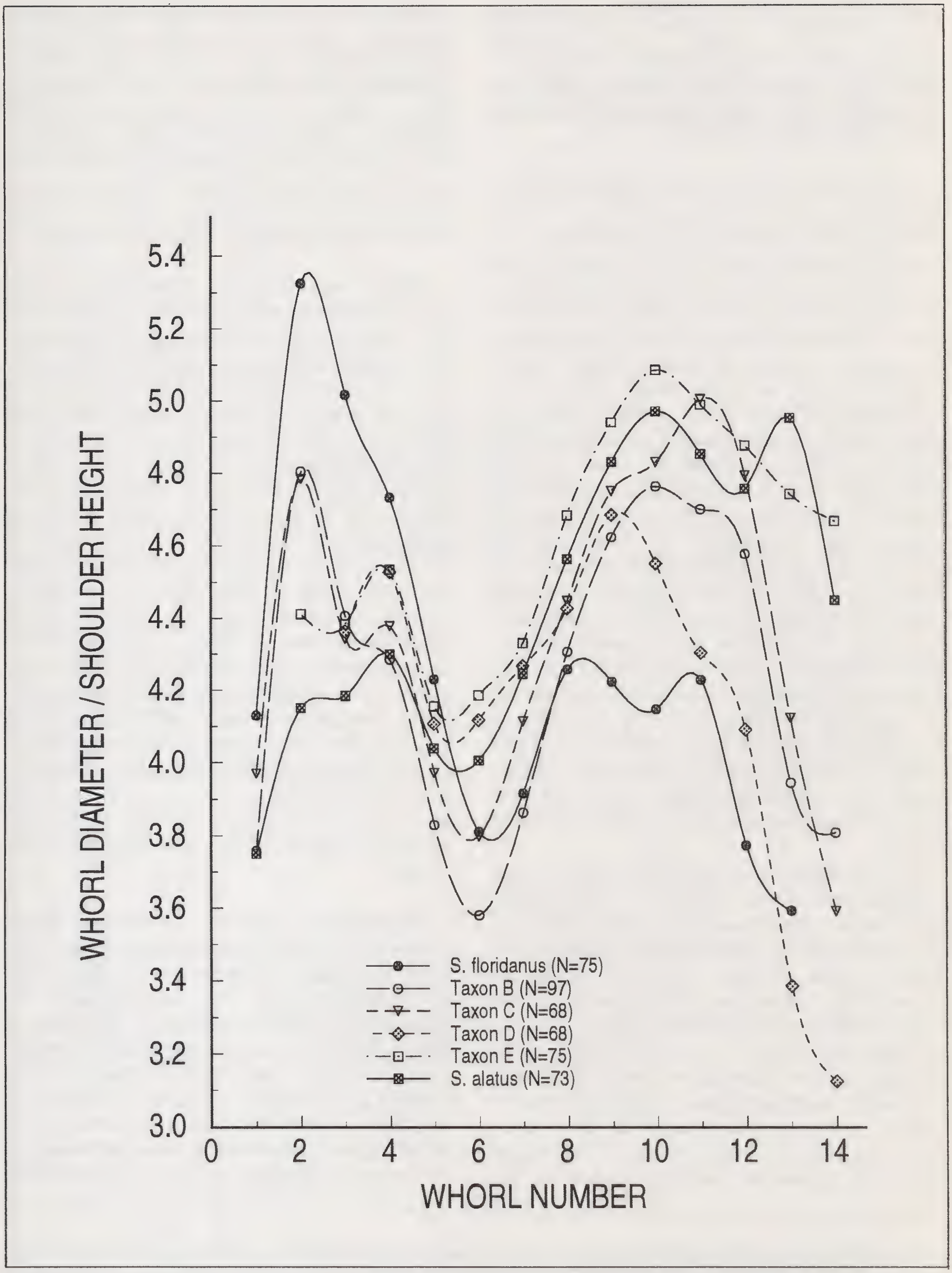
Features Associated with Adult Shell Shape. Text-figure 12 provides a notched box plot comparing the shell heights of the four intervening forms. The shell heights of the *S. alatus* samples having the largest and smallest median values in Text-figure 4-A are included for purposes of comparison. The median values of all of the intermediate forms analyzed fall within the range of variation for that statistic for *S. alatus*. When sufficiently large collections of adult specimens are utilized, none of these forms exhibit the characteristics of *S. floridanus*, suggesting that adult size is a useful characteristic for distinguishing *S. floridanus* from all subsequent fossil and



Text-figure 13. Notched box plot comparing whorl diameters at the end of the protoconch among samples of Florida fossil and Recent *Strombus* forms. The forms included and their sample sizes are as follows: *S. floridanus*, lower Pinecrest beds (N = 36); Taxon B, upper Pinecrest beds (N = 35); Taxon C, Caloosahatchee Formation (N = 29); Taxon D, Bermont Formation (N = 28); Taxon E, post-Bermont units (N = 11); and *S. alatus*, Sanibel Island (N = 51).



Text-figure 14. Comparison of the second order growth curve tracking the mean ratio of whorl diameter to whorl height for samples of Florida fossil and Recent *Strombus* forms. As in Text-figures 2, 8, 9 and 10, the plot conveys information concerning whether the spire profile is seen as concave, convex, or straight sided, with a positive slope indicating a concave aspect. In this and the next three Text-figures, the end-point taxa, *S. floridanus* and *S. alatus*, are represented by solid lines.



Text-figure 15. Comparison of the second order growth curve tracking the mean ratio of whorl diameter to shoulder height for samples of Florida fossil and Recent *Strombus* forms. As in Text-figures 2, 8, 9 and 10, the plot conveys information as to whether individual whorl profiles appear to be tabulate or sloping, with a positive slope indicating an increasingly tabulate aspect over shell development.

recent forms. The data contained in Text-figure 12 seem to support the hypothesis of a single shift in morphological states, with adult sizes going from "*floridanus*-like" to "*alatus*-like" between the lower Pinecrest and upper Pinecrest beds.

Axial and Spiral Ornamentation of Adult Specimens. Axial ornamentation, absent from the body whorl of *S. floridanus,* appears in Taxa B and C in the form of weak curving ribs usually restricted to the shoulder area of the ventral side of the body whorl. The occurrence of such axial ornamentation is rare in these forms, never being present in more than 25% of the specimens of any given sample. On the other hand, specimens of Taxon E from all localities sampled exhibit the same type of blunt spines or knobs on the shoulder of the body whorl as are found on Recent *S. alatus*. The proportion of specimens so adorned ranges from 50% in the Bass Road sample to 96% in the sample collected northeast of Belle Glade. With one possible exception,[12] material from localities containing Bermont material tends to be transitional in this respect. Axial ornamentation on the body whorl is still rare and almost always restricted to the ventral side of the whorl if present at all. However, while weak, the ornamentation is knob-like rather than the curving riblets of earlier forms.

The lirations or rugosities found on the parietal wall of up to 20% of *S. floridanus* specimens are present on almost 50% of the adult Taxon B specimens analyzed. In Taxa C and D their presence drops to about 10%. However, while Taxon C exhibits muted spiral sculpture in all respects on the body whorl, Taxon D tends to have stronger, more persistent external spiral sculpture, submarginate costae, and columellar denticles than any of the other forms included in this study. This vigor does not appear to have extended to the parietal lirations. In post-Bermont Taxon E spiral sculpture is again muted and parietal lirations have yet to be observed.

Hence, with respect to shell sculpture, there appear to be a series of small changes in either the form of the sculpture, the frequency of expression, or both within the four intervening forms of *Strombus* providing support for the hypothesis of incremental morphological change over time.

Adult Color Patterns. The chevron pattern commonly encountered in specimens of *S. floridanus* continues to be observed in a significant fraction of the adult specimens of both Taxa B and C. However, in spite of states of preservation that allow one to see other remnants of color such as the darkening of the leading edges of resting varices on the spire, patterning has been seen on only 2% the body whorls of specimens of Taxon D. When present at all, the pattern appears to be limited to the shoulder area on the ventral side of the whorl. No pattern has been observed in adult specimens of Taxon E. As with the development of parietal lirations, there appears to be a diminution in the expression of this feature over time, with the most significant alteration coming between Taxa C and D. However, the difficulties associated with the observation of color pattern in fossil specimens makes it difficult to characterize the nature of this change with confidence.

Ontogenetic Analysis. Terminal whorl diameters for the protoconchs of the four intervening forms under study are plotted in Text-figure 13. The sample size for Taxon E was fairly small (11), but there is little doubt but what the median protoconch for the form represented by this sample is essentially identical with that of *S. alatus*. The remaining three forms, all of which have, on average, smaller terminal protoconch diameters than *S. floridanus*,

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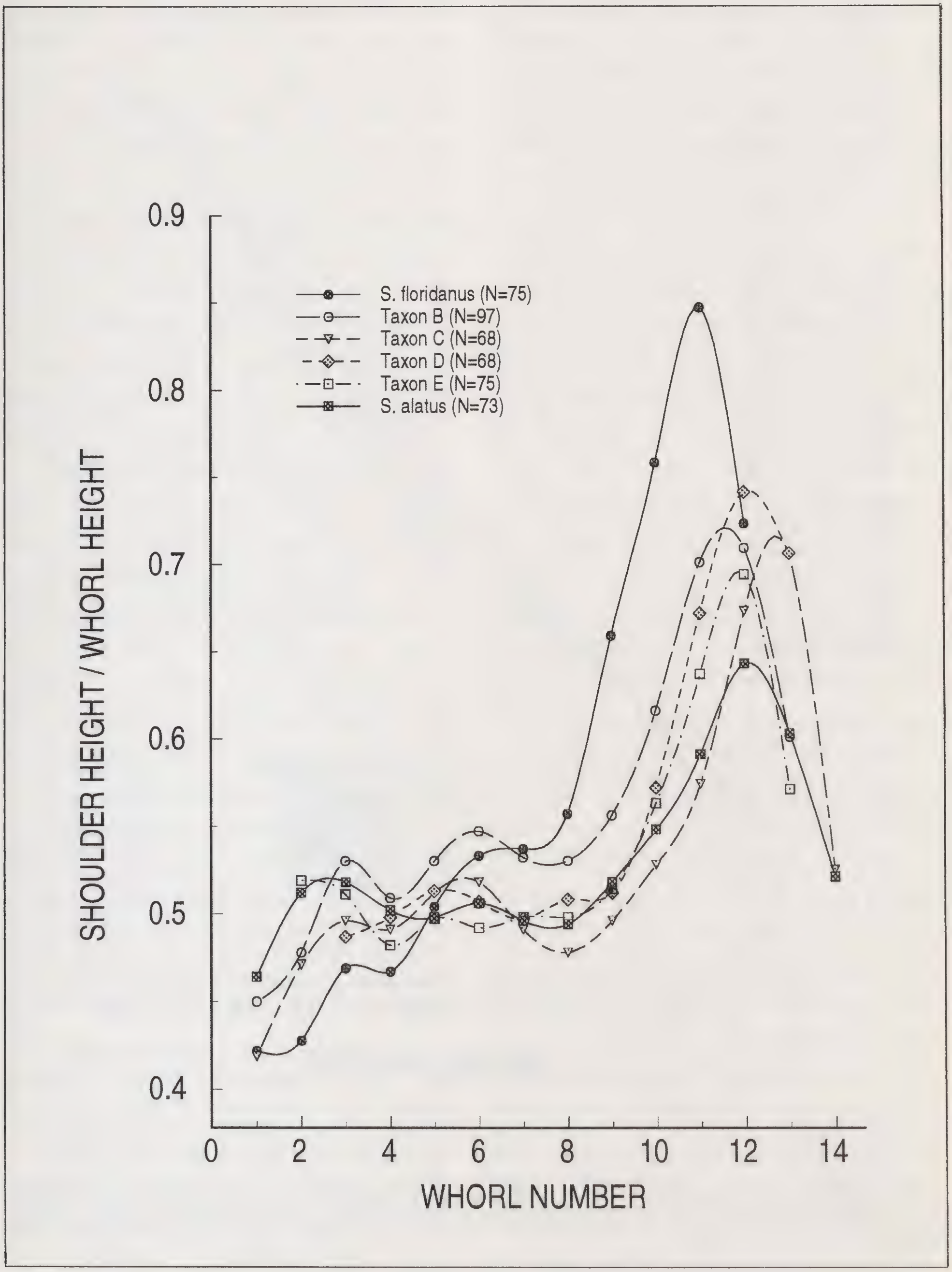
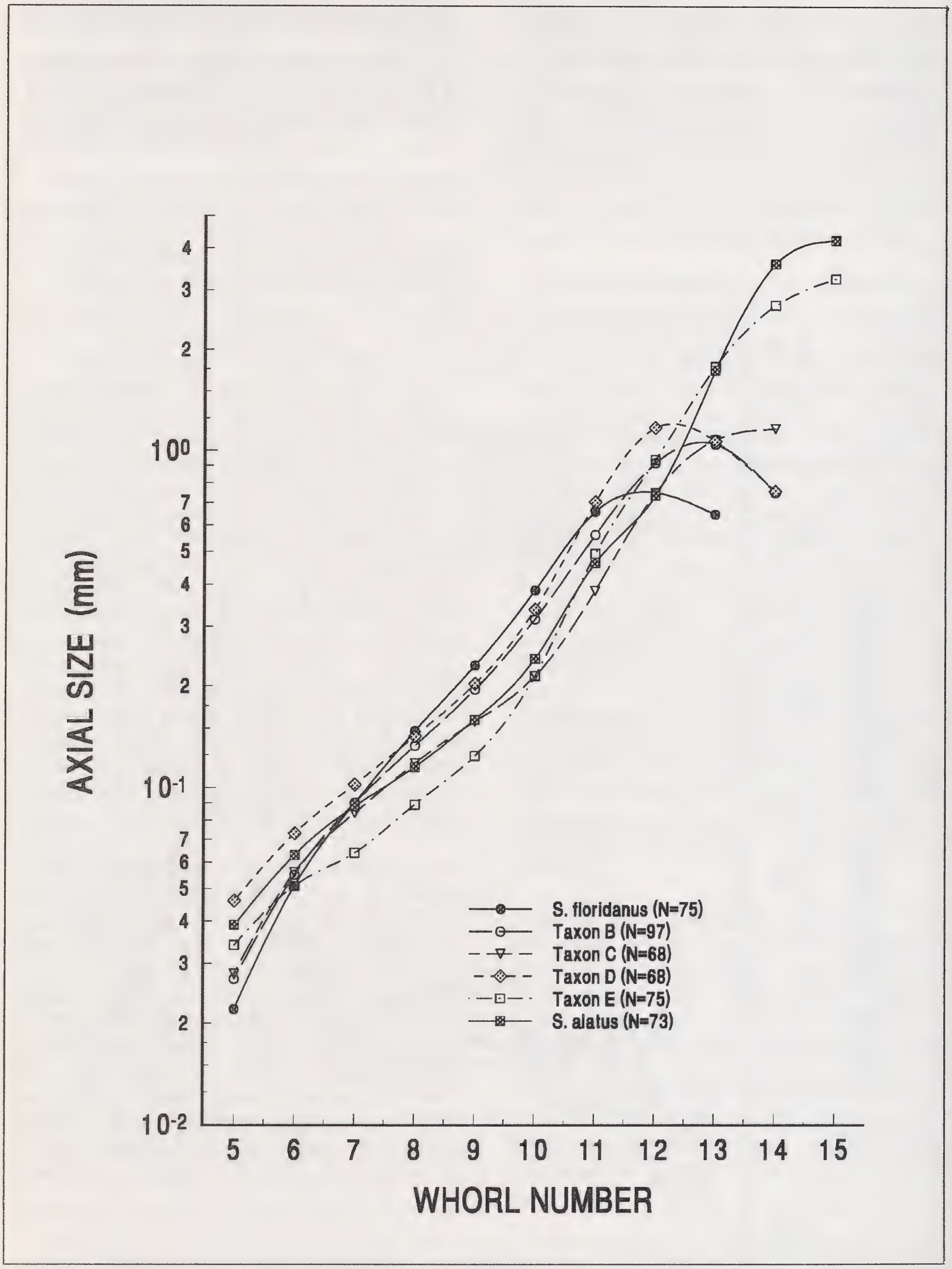
Text-figure 16. Comparison of the second order growth curve tracking the mean ratio of shoulder height to whorl height for samples of Florida fossil and Recent *Strombus* forms. As in Text-figures 2, 8, 9 and 10, the plot conveys information concerning the placement of the suture of the succeeding whorl relative to the whorl periphery and, hence, whether a whorl appears to be turreted or embedded. A positive slope here indicates a spire wherein whorl profiles become increasingly embedded with shell development. >

appear to exhibit a series of incremental reductions in that statistic over geologic time.[13] This offers strong support for the hypothesis of incremental morphologic change over time rather than for a single quantum shift at one point in the time continuum.

To assess other changes in developmental patterns over time, three of the four second order plots that were utilized to





Text-figure 17. Comparison of the mean rates of growth in axial element size (excluding resting varices) over shell ontogeny for samples of Florida fossil and Recent *Strombus* forms.

provide comparative growth profiles of *S. floridanus* and *S. alatus* have been redrawn and expanded in Text-figures 14-16 to include the profiles for the intervening forms. To these three, one of the primary plots has been added portraying the growth in axial element size for these same forms (Text-figure 17). In all plots the mean values for the end-point taxa, *S. floridanus* and *S. alatus*, are denoted by filled circles and squares respectively, connected by solid lines in each case for reference purposes. Mean values for the intervening four forms are marked by a suite of symbols and connecting line types as indicated in the accompanying legends. It should be noted that, even though all of the samples used to develop these profiles were reasonably large, those analyzed to produce the Bermont and post-Bermont curves contained no perfectly preserved juvenile specimens. As a result, protoconch profiles for Taxa D and E cannot be accurately reconstructed at this time.

From the comparative plot of the ratio of whorl diameter to whorl height (Text-figure 8-A) it was determined that a transition from *S. floridanus* to *S. alatus* would have required declining values for both the protoconch and teleoconch maxima over time, reflected in the growth profiles of intervening forms either in the form of a single "quantum" change or in the form of a number of smaller incremental changes. In Text-figure 14 it can be seen that all of the intervening forms do have intermediate teleoconch maxima and, to the extent that it can be determined from the data available, intermediate protoconch maxima as well. However, the teleoconch maxima do not all decline from one form to the next. It should also be noted that the sequence of shifts to the left among the early teleoconch minima over time provide supporting evidence of an incremental reduction in protoconch size among the intervening taxa.

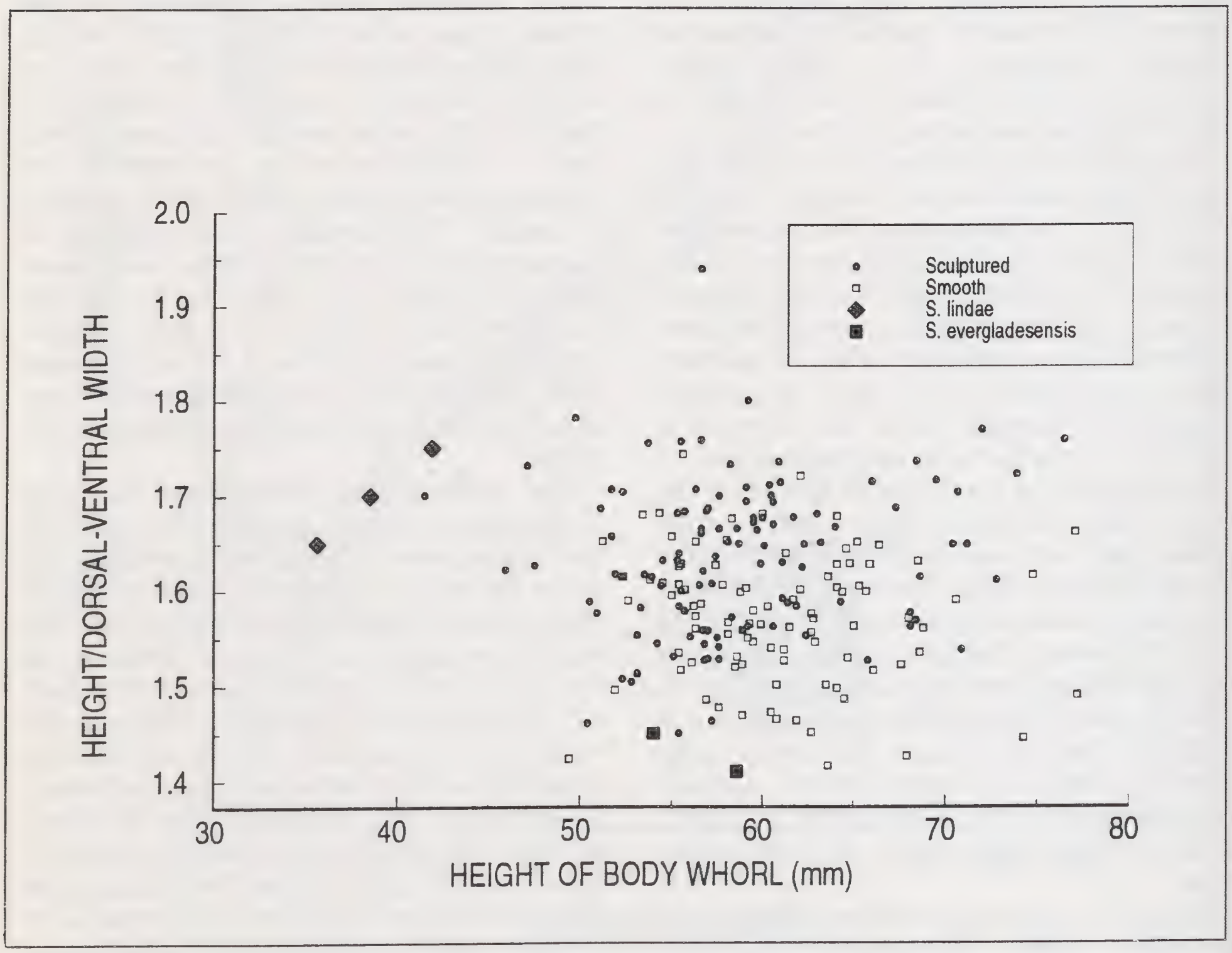
In terms of the plot of whorl diameter to shoulder height (Text-figure 8-B), the transition from *S. floridanus* to *S. alatus* requires a drop in the protoconch maximum and a corresponding increase in the teleoconch maximum, yielding spires whose later whorls become increasingly more tabulate over geologic time. Text-figure 15 presents a comparative set of profiles for this morphologic feature. Although the individual curves themselves are all rather complex, it can be seen that the teleoconch maxima rise quickly to values in the neighborhood of *S. alatus*. The protoconch maxima for the intervening forms are clearly all intermediate in height and, furthermore, the protoconch portions of those curves go through a series of changes as that maximum shifts from the end of whorl two to the end of whorl four. Once again it can be seen that the early teleoconch minimum shifts to the left over time in concert with the reduction in protoconch size.

Considering the ratio of shoulder height to whorl height (Text-figure 8-C), a transition from *S. floridanus* to *S. alatus* requires reductions in the late teleoconch maximum, together with a reduction in the overall slope over the first eight whorls from moderately positive to flat. Text-figure 16 presents a comparative set of profiles for this morphologic feature. Once again it can be seen that the maxima for the intervening forms are all intermediate in height. The complex intermingling of curves over the early whorls makes it more difficult to spot the reduction in overall slope from form to form. However, careful scrutiny shows that Taxon B retains some of the features of *S. floridanus*, while Taxa D and E have the flat characteristics of *S. alatus*.

The most obvious differences between *S. floridanus* and *S. alatus* with respect to the development of axial ornamentation involve the rates of growth from the end of whorl seven through whorl eleven and the maximum axial element size obtained at the end of shell growth (see Text-figure 11). In the case of *S. floridanus* the growth rates over those four whorls is virtually constant and the size of the largest element is well under one millimeter. For *S. alatus* growth is initially much slower but accelerates (*i.e.*, the rate or slope increases) over those same four whorls and the maximum element size (now properly referred to as a blunt spine) is generally in excess of four millimeters. Intervening forms would likely show both a tendency towards accelerated growth rates over whorls eight through eleven and larger ultimate axial element sizes. Text-figure 17 tends to support both of these theses. Not surprisingly,

Taxon E and *S. alatus,* both of which retain axial sculpture on the body whorl, have the largest axial elements. However, all of the other intervening forms have maximum axial sizes that exceed those of *S. floridanus*. Once again, the close proximity of the growth curves makes reading the intermediate growth rates rather difficult. However, if studied carefully it can be seen that the growth rates for Taxon B increase only slightly from the end of whorl seven through the end of whorl twelve. For the other intervening taxa there is a considerable increase in rates over the same set of whorls.

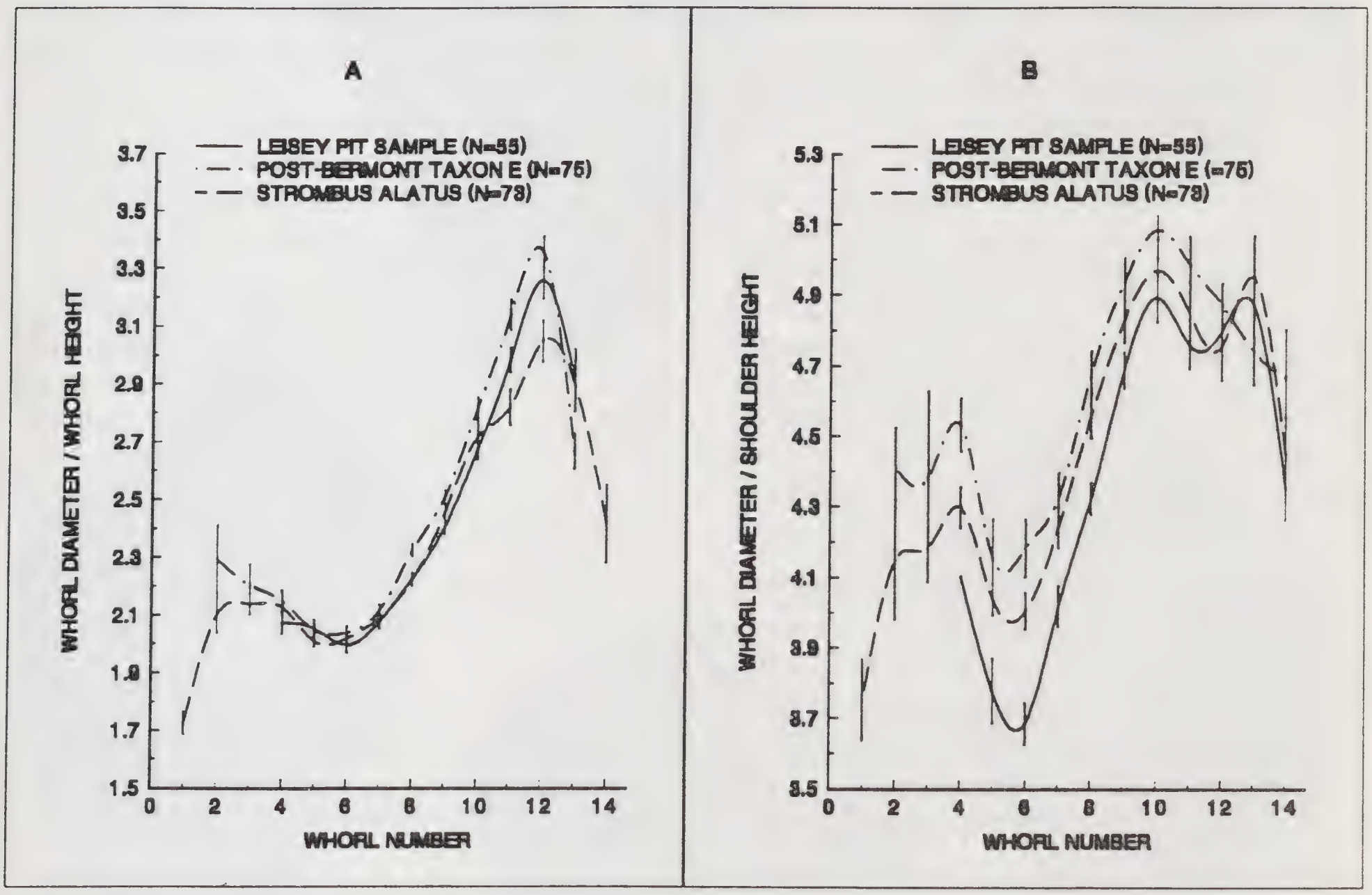
When the four plots making up Text-figures 14 through 17 are analyzed in their entirety, there is little doubt that the intervening forms found in the upper Pinecrest beds, the Caloosahatchee Formation, the Bermont Formation, and the post-Bermont Pleistocene represent a single morphologically changing lineage linking the Pliocene *S. floridanus* with the Recent *S. alatus*. What is more difficult to determine with precision is the exact nature of that change. The data gathered concerning adult size suggests a single shift in that morphological feature between the lower and upper Pinecrest beds. However, the suite of growth profiles does not support the conclusion that other features of ontogeny were coupled to adult size. Of the features present in those growth profiles, only the placement of the teleoconch maxima in Text-figures 14, 16 and 17 appear to



Text-figure 18. Scatter plot showing the relationship among shell size, relative fatness, and the vigor of spiral sculptural expression on the body whorl of 205 adult *Strombus* collected at the Star Ranch borrow pit in Palm Beach County. The height of the body whorl was used as a measure of shell size, while the ratio of body whorl height to dorsal ventral width was used as a measure of relative fatness. For comparative purposes, the type specimens of *S. lindae* Petuch (shaded diamonds) and *S. evergladesensis* Petuch (shaded boxes) are included.

be influenced in part by adult size. The high terminal values of some of the curves in Text-figures 15 and 17 appear to be tied to the extension of spinose axial sculpture to the body whorl of adults, which first becomes prevalent in the post-Bermont form (Taxon E). The analysis of protoconch sizes (Text-figure 13) suggests an incremental reduction in that feature over time. This is supported by, and apparently coupled to, the placement of the early teleoconch minima in Text-figures 14 and 15. Although the data are incomplete, it also appears that there has been a parallel series of incremental changes in larval shell shape over time, as seen particularly in Text-figure 15. Changes in later teleoconch characteristics, as expressed in terms of the heights of teleoconch maxima in Text-figures 14, 15 and 16, are more enigmatic. A chronologically consistent suite of changes in those heights would imply incremental change similar to that which appears to be operating in the larval stage over time, whereas one or more tight clusters could be interpreted as evidence of larger-scale shifts in character states. The curves do not support the former and support for the latter is ambiguous at best. However, the earlier analysis of intraspecific variation among samples of *S. alatus* pointed to the fact that it is the patterns of growth, not specific numerical values, that reoccur from sample to sample. Hence, it would be dangerous to read too much into the numerical values of specific maxima or minima for the samples selected to represent the four intervening fossil forms in this analysis.

In summary, morphologic change in the *S. floridanus/S. alatus* lineage over the past 3.0 to 3.5 million years has been complex. The data clearly do not support the hypothesis of a single change of all morphological characteristics at one point in the geologic record, but they do offer varying degrees of support for the remaining two hypotheses of "decoupled" abrupt



Text-figure 19. Comparison of Leisey Shell pits *Strombus* with the post-Bermont Taxon E and Recent *S. alatus*. [A] portrays changes in the mean value of the ratio of whorl diameter to whorl height over shell ontogeny, while [B] tracks changes in the mean value of the ratio of whorl diameter to shoulder height. The vertical lines indicate the standard errors of those mean values.

changes and incremental change. Changes in larval growth patterns appear to be incremental, while certain features of adult morphology seem to have undergone large-scale changes at different times in the past.

V. CONCLUSIONS

The taxonomic status of analyzed forms.

The most conservative hypothesis based upon the evidence at hand is that the various forms of southern Florida fossil *Strombus* sensu stricto analyzed herein form a single morphologically changing lineage. There is neither morphologic evidence for any branching speciation event among these forms during the past 3.0 to 3.5 million years, nor any evidence from *in situ* collections that the forms coexist in the same biostratigraphic units.[14] The growth profiles, together with the data accumulated concerning adult sizes, demonstrate that *S. floridanus*, as found in the *Cancellaria* zone of the Jackson Bluff Formation and lower Pinecrest beds, is morphologically distinct from all later forms, supporting Mansfield's separation of that taxon from the Recent *S. alatus*. The failure of the data to support the hypothesis of a single abrupt shift in all morphological characteristics studied suggests that subsequent forms should not all be equated with *S. alatus*. However, in terms of protoconch size, the presence of shoulder spines on the body whorl of adults, and the overall similarities in growth profiles, it does appear that the post-Bermont form, Taxon E, can be grouped within *S. alatus*. Taxa B, C, and D then would appear to represent one or more morphologically distinct chronospecies ranging from the upper Pinecrest beds through the Bermont Formation.

Are there any characteristics that would allow workers in the field to separate Taxa B, C, and D on the basis of cursory visual inspection? For the Bermont Taxon D two features can be noted: (1) the nature and strength of the spiral sculptural elements on the body whorl of adult specimens; and (2) the presence of pronounced resting varices on the last three teleoconch whorls of adults. Specimens of Taxa B and C tend to have much less pronounced resting varices on the later whorls and very muted spiral sculpture on the body whorl both externally and within the aperture of adult specimens. Conversely, many Bermont specimens exhibit exterior spiral sculpture that is both persistent and complex over much of the dorsal surface of the body whorl and is particularly strong on the expanded adult lip. With the exception of the parietal rugosities, the sculptural elements inside the aperture are equally robust in this form.

It may well be that these more robust sculptural features are the result of predation; a significant fraction of the robustly sculptured adult specimens at the Bermont sites surveyed exhibit breakage and repair, suggesting unsuccessful predation. At some point in time after reaching adulthood, individuals were attacked by a predator (probably a crab) capable of breaking back the thickened adult lip (sometimes 4 mm in thickness), often as far as a substantially thickened resting varix some

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PLATE 2

Figures

1-2. *Strombus floridanus* Mansfield
   1. (X 1.2) Holotype – *Strombus pugilis floridanus* Mansfield, 1930. USNM 370260; height 62 mm, diameter 36 mm (young adult specimen). Locality: USGS station 3422, Harvey Creek, Leon County, Florida; *Cancellaria* zone of the Jackson Bluff Formation.
   2. (X 1) USNM 483765; height 61.1 mm, diameter 33.0 mm. Locality: Unit 7, APAC Pit, Sarasota, Florida (= TU 1000); lower Pinecrest beds.
3. *Strombus* sp. aff. *S. evergladesensis* Petuch (X 0.8)
   USNM 483766; height 85.1 mm, diameter 49.7 mm.
   Locality: Unit 4, APAC Pit, Sarasota, Florida (= TU 1000); upper Pinecrest beds.

(Diameter of all specimens includes the expanded adult lip)

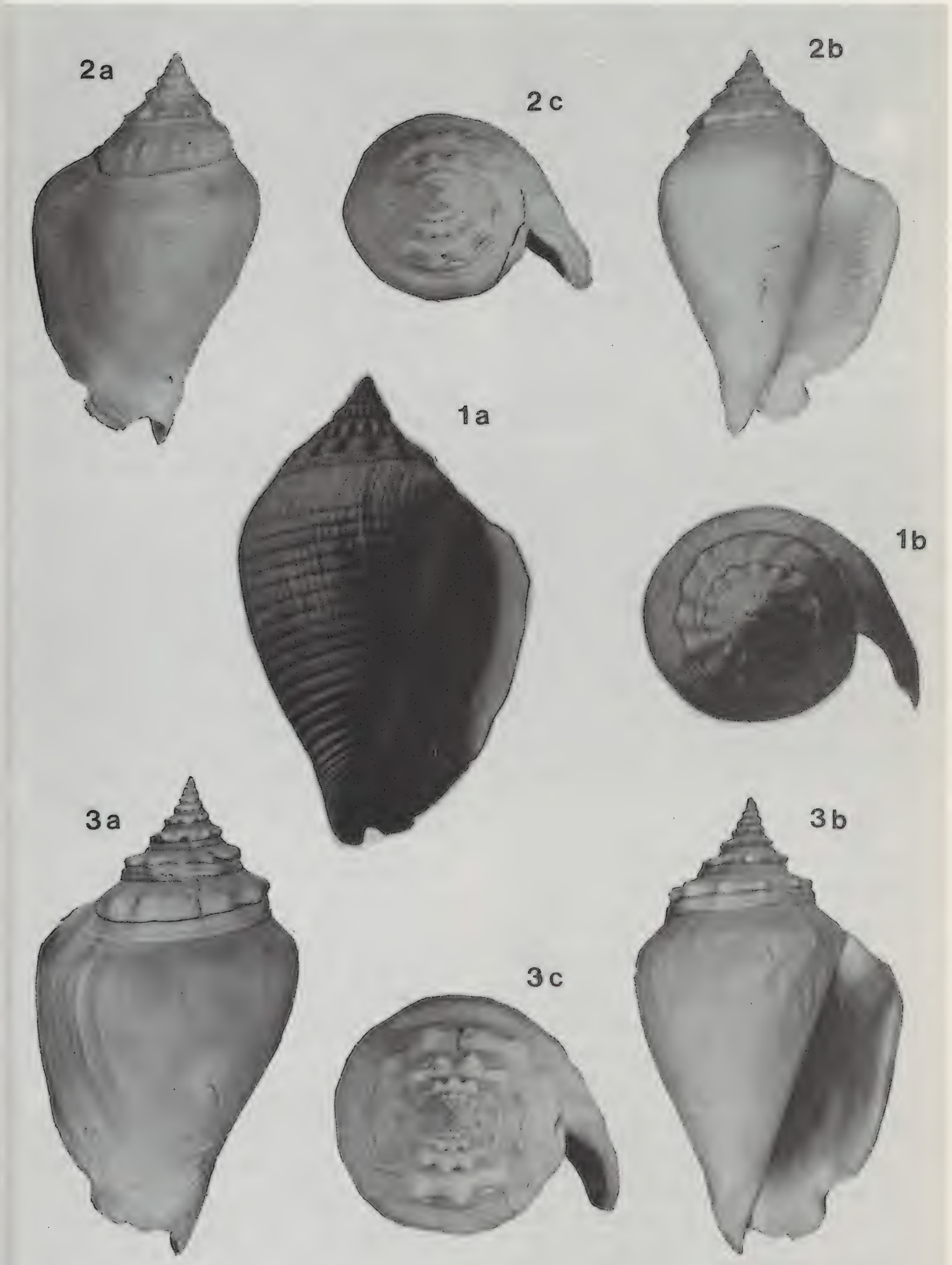

PLATE 2

220 degrees behind the terminal point of growth. Subsequent repair of many of these the severely damaged body whorls indicates that this predation was often unsuccessful. The spires of these individuals also tend to yield evidence of multiple earlier unsuccessful attacks on the juveniles as they matured. Evidence of such predation is rare among the generally less robustly sculptured forms from other biozones. It might be hypothesized then that thickened resting varices and spiral sculpture provide extra shell strength, protecting the animal from both shell crushing predators and those that attempt to peel back the shell from the lip, and that the retention of these features in adulthood is a response to specific predators capable of attacking mature *Strombus*.[15]

The bold chevron color pattern so common in all forms up through Taxon C is seen rarely in Taxon D. The variables involved in the preservation of color pattern in fossil specimens would seem to make conclusions based upon the absence of pattern in certain fossil forms risky. However, specimens from the same collecting localities of other taxa that tend to retain their color patterns over time (*e.g.*, *Conus* and *Scaphella*) are often clearly marked. Hence, one should probably consider the lack of pattern to be real rather than an artifact of preservation and a useful diagnostic tool.

It has been noted that there appears to have been small incremental reductions in protoconch size in going from Taxon B to Taxon C to Taxon D. Text-figures 14 and 15 indicate additional developmental differences between Taxa C and D that affect the overall shape of the protoconch. It should be pointed out that no specimens of Taxon D have yet been found with perfectly preserved protoconchs, making it impossible to construct a complete profile of that form. In addition, the number of specimens of Taxa B and C with perfectly preserved protoconchs analyzed was small; 4 in the former case and 10 in the latter. Finally, even if the differences noted are accepted as expressions of real differences in larval ontogeny over time, cumulative spire wear limits their usefulness to the microscopic analysis of large samples of juvenile *Strombus*.

The teleoconch portions of the growth profiles deal with characteristics more useful for separating adult *Strombus* and more amenable to visual comparison with the unaided eye. Addressing first Taxon D, it can be seen that the general form of the teleoconch maximum in Text-figure 15 is somewhat different than those for Taxa B and C. In this respect Taxon D is morphologically intermediate between *S. floridanus* and Taxon B. The late protoconch and early teleoconch portions of Text-figure 16 show subtle differences between Taxa B and C, and, in Text-figure 17, the axial element growth rates over whorls 8 through 12 are more constant for Taxon B than they are for Taxa C or D. In these two instances, the growth characteristics of Taxon B appear to be transitional in nature, separating *S. floridanus* from all later forms.

In summary, there exist a reasonably large suit of characteristics, some of them developmental and some expressed in the adult state, that can be referred to in distinguishing between Taxa C and D, and the weight of evidence suggests that these two forms should provisionally be considered as distinct chronospecies. On the other hand, there are but three subtle developmental differences separating Taxon B from Taxon C. It would, therefore, be prudent to consider the upper Pinecrest and Caloosahatchee forms to be a single taxon (*i.e.*, Taxon B = Taxon C).

The status of recently proposed taxa.

Petuch (1991) has described two *Strombus* taxa purporting to come from the post-Caloosahatchee, lower Pleistocene of southern Florida, *Strombus evergladesensis* and *Strombus lindae*.[16] Although it is reasonable to assume that these taxa are related in some way to the forms referred to herein as Taxa B, C and D, Petuch's work poses significant problems, both with respect to the taxa themselves and with respect to the biostratigraphic horizons they supposedly inhabit.

Petuch (1990) informally introduced a biostratigraphic unit entitled the Holey Land Limestone, which he subsequently suggested might represent "a new formation intermediate between the older Ca-

loosahatchee Formation and the younger Bermont Formation" (Petuch, 1991, p. 6). Under the discussion of these units in the latter work he lists *S. evergladesensis* among the index fossils for the supposedly younger Bermont Formation and *S. lindae* as an index fossil for the underlying Holey Land unit, implying that the two taxa did not coexist in geologic time and that *S. evergladesensis* is the younger taxon. Seven pages later, however, he contradicts himself, placing the type locality of *S. evergladesensis* in the Holey Land unit rather than in the Bermont Formation. The type locality for *S. lindae*, although different from that of *S. evergladesensis*, is also placed in the Holey Land Unit, implying that the two taxa are sympatric. In a popular work published a year later (Petuch, 1992) there is no mention of the Holey Land unit at all and the two *Strombus* taxa under consideration are portrayed as sharing the same habitat in the Bermont Okeechobean Sea.

In spite of the fact that Petuch places the two new *Strombus* taxa in the same stratigraphic unit (albeit a different one) on at least two of three occasions, he does not compare one with the other while describing and discussing either species. Instead, he compares each with a form or subspecies of *S. alatus* (probably the post-Bermont Taxon E) that he seems to think coexisted with both *S. evergladesensis* and *S. lindae*. Using Petuch's language (1991, pp. 14, 15), I have sought to construct, out of these pair-wise comparisons with *S. alatus*, a set of diagnostic characteristics for the two taxa:

Adult Size – *Strombus lindae* is small (all specimens referred to by Petuch being under 70 mm), whereas *S. evergladesensis* is typical of the subgenus (*i.e.*, around 80 mm).

Outline – *Strombus lindae* is elongated, slender with high, elevated, protracted spire, whereas *S. evergladesensis* is very bulbous, inflated or globose, but having a spire with the early whorls elevated, protracted and scalariform. (This would seem to suggest a more concave spire aspect for *S. evergladesensis* than for *S. lindae*.)

Axial Elements – *Strombus lindae* has blunt, knob-like spines on the penultimate whorl and occasionally obsolete spines on the dorsum of the body whorl. In *S. evergladesensis* the axial sculpture becomes obsolete and disappears on the penultimate whorl so that the shoulder of the body whorl is without axial ornamentation.

Spiral Sculpture on the Body Whorl – *Strombus lindae* is said to be heavily ornamented with large, evenly spaced spiral cords, although the mid-dorsum is acknowledged to have a smooth spot. *Strombus evergladesensis*, by contrast, has a body whorl that is smooth and polished with spiral sculpture limited to the siphonal canal.

Stromboid Notch – Deep and well-developed in *S. lindae*, but shallow and poorly developed in *S. evergladesensis*.

The present study has shown that adult size and relative fatness are characteristics of dubious value in separating the forms of *Strombus* sensu stricto present in southern Florida, especially when statistical analyses of large samples are not carried out. Petuch's descriptions appear to be based upon very small data sets, in spite of the abundance of *Strombus* at almost all collecting localities. The description of *S. lindae* is based upon four specimens while that of *S. evergladesensis* is based upon three. It is claimed in the discussion of *S. lindae* that it is the smallest conch shell known from the Florida Pleistocene (Petuch, 1991, p. 15). The holotype is recorded as 54 mm (which it is). However, when the holotype is figured once again in his 1992 work, it is said to be 42 mm (Petuch, 1992, p. 42, figure 21, nos. 2, 6). On the next page in that work it is claimed that an unnamed Bermont *Strombus* reaches adulthood at 25 mm.[17] The holotype of *S. evergladesensis* was reported by Petuch in 1991 to be 72 mm (it is, but about 5 mm of the anterior end is missing). Yet in 1992 this same specimen is listed as being 68 mm (Petuch, 1992, p. 42, figure 21, no. 3). These discrepancies throw doubt on taxa supposedly differentiated primarily by adult size.

In order to test the correlations among the individual characteristics cited by Petuch, a sample consisting of 205 adult *Strombus* was analyzed from a single collecting locality for this study. The Star Ranch borrow pit (TU 1536) is located approximately 18 kilometers due north of the Griffin Brothers Quarry, type locality for *S.*

evergladesensis, and approximately four kilometers northwest of the type locality for *S. lindae*. The excavation at that site has penetrated the sandy facies of the Bermont, the Holey Land Limestone, and into the underlying Caloosahatchee Formation. Since the pit itself is flooded, all collecting at that site is restricted to spoil piles that contain a mixture of Bermont and Caloosahatchee index fossils. Specimens assignable to each of Petuch's taxa were present in numbers.

Text-figure 18 shows the results of this analysis, plotting a measure of relative "fatness" (the ratio of the height of the body whorl to the dorsal-ventral width of that whorl, the same ratio that is plotted in Text-figure 4-C), against a measure of shell height, in this case the height of the body whorl. Those specimens exhibiting strong internal and external spiral sculpture are differentiated from those specimens having a smooth body whorl with weak or absent internal spiral elements, the former being marked by small solid circles, the latter by small open boxes. According to the criteria set forth above for differentiating Petuch's two Bermont taxa, one would expect a cluster of specimens in the top left hand portion of the plot marked by solid circles representing *S. lindae* (*i.e.*, small, slender, heavily sculptured specimens), and another cluster in the bottom right hand portion of the plot marked by open boxes representing *S. evergladesensis* (*i.e.*, large, bulbous, smooth-surfaced specimens). Data for the holotype and two deposited paratypes of *S. lindae* (solid diamonds), together with the holotype and one deposited paratype of *S. evergladesensis* (large solid boxes), are included on the scatter plot for reference. Several points are immediately apparent. First, the specimens do not sort themselves into two morphologically distinct populations. Second, there is no discernable correlation between adult shell size and fatness or between shell size and the strength of expression of spiral sculpture. There is only the weakest of correlations between shell shape (*i.e.*, fatness) and the expression of spiral sculpture. Third, Petuch appears to have chosen the most extreme forms available to him to describe his two taxa. From the evidence contained in this plot one cannot rule out the possibility that *S. lindae* and *S. evergladesensis* simply represent two extreme forms of the same morphologically variable Bermont taxon. If this is the case, then *S. evergladesensis* would have priority. And, since it has been demonstrated herein that the Bermont Taxon D is a distinct chronospecies, *S. evergladesensis* would be equated with that form.

Other interpretations, however, are also possible. Given the fact that both Bermont and Caloosahatchee index fossils are pre-

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PLATE 3

Figures

1. *Strombus evergladesensis* Petuch (X 1.2)
   CM 35698 (holotype); height 72.8 mm (anterior tip missing), diameter 46.6 mm.
   Locality: Griffin Brothers Quarry, Broward-Palm Beach County line, Florida; Holey Land Unit (= Bermont Formation?).
2. *Strombus* sp. aff. *S. evergladesensis* Petuch (X 0.8)
   USNM 483767; height 77.5 mm, diameter 43.8 mm.
   Locality: DeSoto Shell Pit # 3, DeSoto County, Florida; Caloosahatchee Formation.

3-4. *Strombus lindae* Petuch

3. (X 1) Holotype – *Strombus lindae* Petuch, 1991.
   CM 35700; height 53.4 mm, diameter 28.1 mm.
   Locality: North New River Canal, Palm Beach County, Florida; Holey Land Unit (= Bermont Formation?).
4. (X 0.8) USNM 483768; height 75.6 mm, diameter 42.9 mm.
   Locality: North New River Canal (about 4 km nw of the type locality), Palm Beach County, Florida; Bermont Formation.

(Diameter of all specimens includes the expanded adult lip)

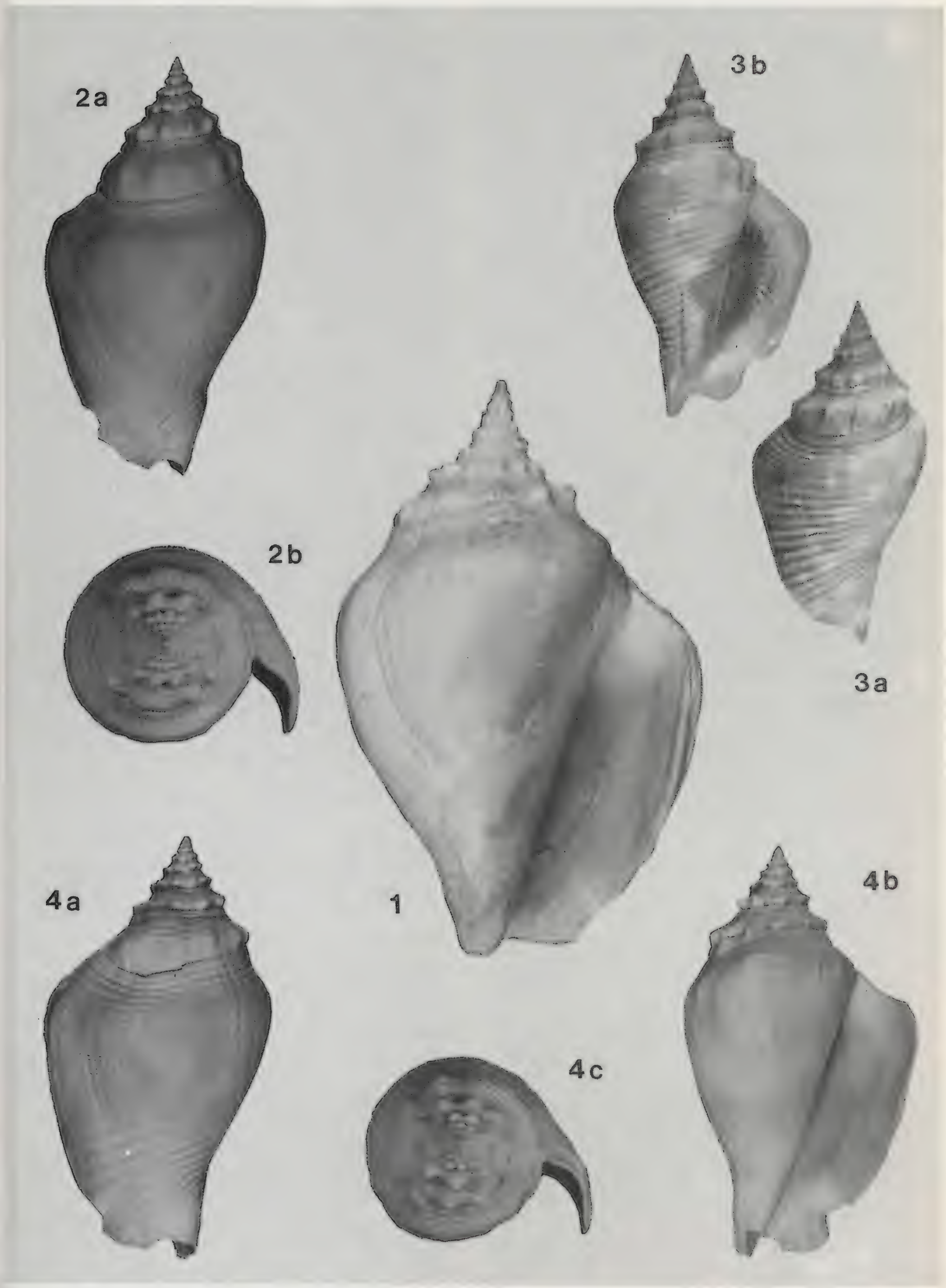

PLATE 3

sent at the site, the Star Ranch sample utilized above almost certainly contains material from different biostratigraphic units. Petuch's material undoubtedly also came from spoil collecting making it quite possible that his two taxa are not sympatric. If this is the case, then several hypotheses open up involving the Caloosahatchee Formation, the Holey Land unit, and the sandy shell marl facies of the Bermont Formation. Petuch himself offered one possibility when he included *S. lindae* as an index fossil for the Holey Land unit and *S. evergladesensis* as an index fossil for the supposedly younger Bermont Formation (Petuch, 1991, p. 7). However, this author thinks it much more likely that, if the two forms do come from different biostratigraphic units, that it is *S. lindae* that resides in sandy shell marl of the Bermont Formation, while *S. evergladesensis* is found in some lower unit, either the Caloosahatchee Formation or the lower Bermont Holey Land unit.

The sample utilized in this study to create the growth profile for the Bermont Taxon D was collected from a location (F07) along the North New River Canal about one kilometer northeast of the Star Ranch pit and roughly four kilometers upstream from the type locality for *S. lindae*. Like the material taken from the *S. lindae* type locality, this sample was collected from spoil dredged from the North New River Canal in the early 1980's. If the presence of spiral sculpture on the body whorl is a valid distinguishing characteristic of *S. lindae*, then the specimens utilized to create the growth profile for Taxon D all appear to be referable to that taxon. The absence of both *S. evergladesensis* and Caloosahatchee index fossils at this locality, would seem to be significant. In all probability the canal dredging did not reach the same depths as the borrow pit nearby. Hence, Petuch's *S. evergladesensis* might represent very fat specimens of the underlying Caloosahatchee form (Taxon C) or it might represent an allied form confined to the basal units of the Bermont Formation. The fact that only one of the 93 specimens from the Star Ranch pit referred to *S. evergladesensis* exhibited even a hint of chevron color pattern supports the second interpretation.[18]

Further support for this interpretation comes from material taken from the upper shell bed along Shell Creek (TU 539A), the type locality for the Bermont Formation. Although the 17 specimens available for study yield no information on the protoconch whorls, in terms of the gross shell characteristics that have been used to distinguish *S. evergladesensis* from *S. lindae*, all of the Shell Creek specimens more closely resemble the former. The distinctive chevron color pattern often present in upper Pinecrest and Caloosahatchee specimens was not observed in this Shell Creek sample.

It is clear that Petuch's *S. lindae* represents the form identified herein as Taxon D, even though most of the characteristics used by him to distinguish the taxon are suspect. *Strombus lindae* can, therefore, be seen as a valid taxon. Whether one equates *S. evergladesensis* with the upper Pinecrest and Caloosahatchee form (Taxon B = Taxon C) at this point in time depends upon the importance one places in the apparent rarity of color patterns in this taxon. In other respects the taxon would seem to capture the salient features of the older Caloosahatchee and upper Pinecrest forms. The situation could be clarified if it were possible to create complete growth profiles for *S. lindae* and *S. evergladesensis*. Until this can be accomplished the most conservative position would be to equate *S. evergladesensis* with Taxa B and C, considering its distribution in the fossil record to range from the upper Pinecrest beds to at least the lower portion of the Bermont Formation. Again, if the characteristics used to separate Taxon D from Taxa B and C are not deemed to be sufficient for that purpose, then all three forms should be equated with *S. evergladesensis*, with *S. lindae* being considered a form of that taxon.

Chronostratigraphy.

The APAC Pit. In the past few years a team of investigators from the University of Florida have applied a multi-faceted approach to the Pliocene/Pleistocene geochronology of selected south Florida sites (Webb *et al.*, 1989; Jones, 1990; Jones *et al.*, 1991). For the APAC study (Jones *et*

al., 1991), paleomagnetic assessments were undertaken and strontium isotope ratios measured for all of the eleven units identified by Petuch (1982), and ostracode samples were collected for all but the lowest unit. The critical unit, however, was Petuch's "black layer" (Unit 4), an organically-rich marine deposit containing abundant vertebrate remains. The mammalian remains present in that unit, their concurrent range elsewhere in the country, and the reversed magnetic polarity associated with all units, suggested an age for Unit 4 ranging from 2.5 Ma to 2.1 Ma (Jones *et al.*, 1991, p. 642). Of the units above the black layer, only Unit 1 appeared to be of appreciably different age. Based upon strontium isotopic ratios, a rather broad age range of 2.0 Ma to 1.0 Ma was proposed for that unit (Jones *et al.*, 1991, p. 644). The ostracode fauna present in the units below Unit 4 occur elsewhere in coastal plain deposits dated between 3.5 Ma and about 2.8 Ma. Based upon this and the paleomagnetic evidence, the authors came up with three possibilities for what has been referred to herein as the lower Pinecrest beds at APAC:

> "(1) if the faunas are 2.5 Ma or younger, these units could be placed in the lower Matuyama Chron, along with Units 4 and above; (2) if the faunal age is truly around 3 Ma, a correlation with the Kaena or Mammoth Subchrons within the Gauss Chron is possible; or (3) if the faunal age is closer to 3.5 Ma, these units might belong in the upper portion of the Gilbert Chron." (Jones *et al.*, 1991, p. 645).

In the present study of *Strombus* sensu stricto, samples were collected for study from Units 2, 4, 6 and 7 at APAC and the equivalent units at the nearby Quality Aggregates operation. Analysis of that material demonstrated clearly that, at least in the case of *Strombus*, the fauna of the lower units is not the same as that of Unit 4 and above. *Strombus floridanus*, described from the *Cancellaria* zone of the Jackson Bluff Formation, was present in Units 6 and 7, but not in the upper units. From Unit 4 upward it is replaced by a form referred to herein as Taxon B that is not found in the Jackson Bluff Formation. In terms of shell morphology Taxon B is more closely related to the Caloosahatchee form (Taxon C) and even to the Bermont form (Taxon D) than it is to the underlying *S. floridanus*. This suggests a hiatus between Unit 4 and the units below, lending support to either the second or the third of the hypotheses above, or to some combination of the two.

Lyons (1990, 1991) has demonstrated that Unit 1 at APAC contains a Caloosahatchee-age molluscan fauna. Although *Strombus* specimens have not been collected from that unit for study, one would not expect them to be of use in clarifying the relationship between this unit and underlying units, given the morphological similarity between the Caloosahatchee Taxon C from other localities and the upper Pinecrest Taxon B from APAC. Helium-uranium dates by Bender (1973) in the range of 1.9 Ma to 1.7 Ma for corals taken from another Caloosahatchee site, together with the evidence presented by the University of Florida team concerning the age of the Leisey Pit strata to be discussed below, support an age for Unit 1 towards the older end of the 2.0 Ma to 1.0 Ma range presented by Jones *et al.*, probably before the onset of the Olduvai Subchron at 1.88 Ma.

The Leisey Shell Pits. Extensive vertebrate bone beds separating massive marine shell beds were uncovered during the 1980's in two of three adjacent borrow pits excavated near Little Cockroach Bay in southern most Hillsborough County (Webb *et al.*, 1989). The accumulated weight of evidence would seem to restrict a substantial portion of the Leisey section, including the bone beds and the underlying marine deposits, to an age range of 1.66 Ma to 1.4 Ma (Webb *et al.*, 1989, p. 109). Based upon the presence of small numbers of three fossil species thought to be index fossils for the Bermont, the authors tentatively referred all of the marine sections below the bone beds, as well as some above the bone beds, to the Bermont Formation. However, they admitted that most of the taxa identified with more southerly Bermont sites are absent from the Leisey fauna, suggesting that this might be due either to temperature differences or to age differences, with the strata at the Leisey Pits being somewhat younger than their southern counterparts.

Specimens of *Strombus* sensu stricto are among the most common gastropods present in the Leisey fauna, although juveniles with well-preserved protoconchs are rare. A total of 115 specimens were studied for this paper, 100 adults and 15 juveniles. Of the 115 specimens, 39 were borrowed from the collections of the Florida Museum of Natural History and 29 of those were collected *in situ* during the field work carried out in conjunction with the Webb *et al.* study. The remaining 86 specimens were collected from spoil. Only one of the 100 adult specimens could be referred to the Bermont form described by Petuch as *S. lindae*. It was collected from spoil in Pit #03. Of the remaining 99 adults, 73 have shoulder spines on the body whorl and appear to be identical to the form identified herein as Taxon E (= *S. alatus*) present in the post-Bermont deposits of southern Florida. Among the specimens collected *in situ* from different horizons within the Leisey pits, spined specimens were found above, below, and in the bone beds. While the remaining 26 adults that do not have shoulder spines on the body whorl could represent Petuch's supposed Bermont *S. evergladesensis*, it is much more likely that they are simply smooth shouldered specimens of *S. alatus*. Recall that the fraction of spined adults among sampled populations of Taxon E ranges from 50% to 96%.

To seek further clarification concerning the identity of the Leisey form of *Strombus*, 55 specimens, including all of those borrowed from the Florida Museum, were analyzed to obtain a growth profile. These were then compared with the profiles developed for Taxon E and for Recent *S. alatus*. Two of these comparative second order plots are presented in Text-figure 19 to show the similarities among the three forms. There would seem to be little doubt that all three profiles belong to the same species, *S. alatus*.

One is forced to conclude that a large majority of the *Strombus* at the Leisey Shell Pits, both above and below the bone beds, represent *S. alatus* and not either of the forms assigned by Petuch to the Bermont Formation, *S. lindae* or *S. evergladesensis*. *Strombus lindae*, the one taxon unquestionably identified with the Bermont Formation at more southerly locations, is present in the Leisey pits, but appears to be very rare. As pointed out above, although some of the specimens lacking shoulder spines on the body whorl might represent *S. evergladesensis*, the form found in the upper shell beds at Shell Creek, their presence with *S. alatus* suggests that they are simply spineless specimens of that taxon.

Given that Taxon E (*S. alatus*) is present even in the lower shell beds, it is unlikely that much of the Leisey section is referable to the Bermont biozone, as it is defined either at the type locality or at sites south of Lake Okeechobee. Whether one wants to consider the fauna present as "younger" Bermont or post-Bermont is of little real significance here. The important point is that the University of Florida studies would seem to compress a number of biozones representing a significant amount of evolutionary activity and/or geographic replacement into a rather short time interval. Units 4 through 2 at APAC are regarded by most investigators to be part of a biostratigraphic unit known as the Pinecrest beds (albeit the upper Pinecrest beds

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PLATE 4

Figures

1-3. *Strombus alatus* Gmelin (X 0.8)

1. Hargreave Collection; height 89.9 mm, diameter 50.5 mm.
   Locality: Sanibel Island, Florida; Recent.
2. Hargreave Collection; height 78.6 mm, diameter 45.5 mm.
   Locality: Sanibel Island, Florida; Recent.
3. USNM 483769; height 71.6 mm, diameter 44.3 mm.
   Locality: Temporary excavation, Bass Road, Lee County, Florida; Ft. Thompson Formation?

(Diameter of all specimens includes the expanded adult lip but not shoulder spines)

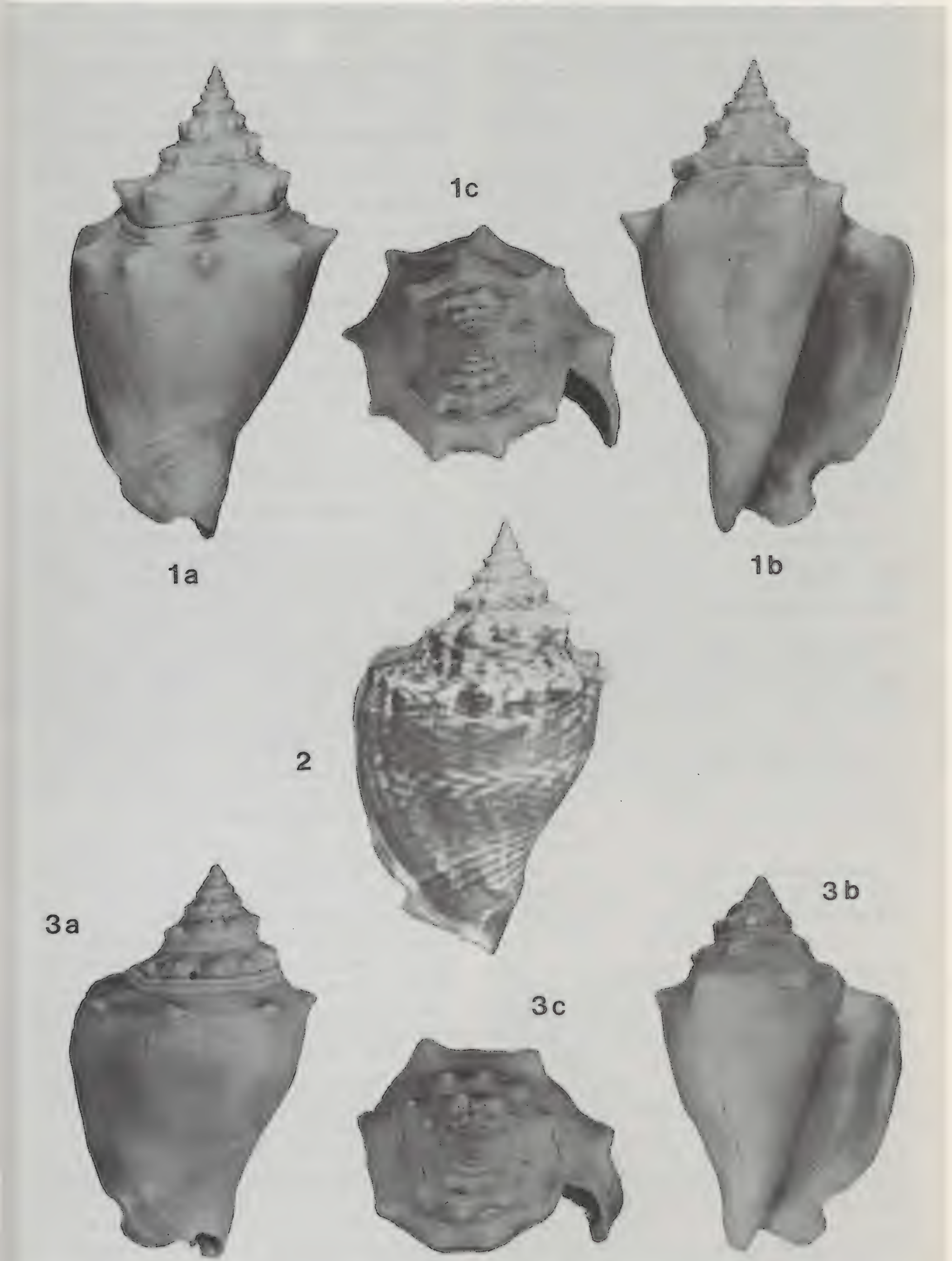

PLATE 4

by some). These units appear to be between 2.4 and 2.1 million years old. Unit 1 at APAC has been referred to another well-established biostratigraphic unit, the Caloosahatchee Formation. As pointed out above, a reasonable guess as to the age of APAC Unit 1 would be between 2.0 and 1.88 million years old. The bone beds and lower shell beds at the Leisey pits have been dated at between 1.66 Ma and 1.4 Ma, and it is suggested herein, based upon the *Strombus* fauna, that this represents a post-Bermont (or younger Bermont) assemblage. If this is the case, then somewhere in between 1.88 Ma and 1.66 Ma the "real" Bermont biozone must be accommodated, not to mention the Holey Land unit if it proves to be something other than simply a limestone facies of the Bermont. Put another way, in a one million year interval or less (*i.e.*, from 2.4 Ma to 1.4 Ma), the marine faunal assemblages of southern Florida passed from upper Pinecrest, to Caloosahatchee, to Bermont, to something beyond Bermont. Morphologic change within the *Strombus* lineage studied here appears to have gone from *S. floridanus* to *S. alatus* in two million years or less, and from Taxon B to *S. alatus* in about one million years. Significantly, the lineage does not seem to have undergone any further morphologic change for the past 1.4 million years, in spite of the environmental pressures associated with the coming and going of ice ages.

Observations Concerning Other Pinecrest Localities. As part of this investigation an attempt was made to study *Strombus* samples taken in years past from localities identified as containing a Pinecrest fauna by Olsson (1964) in his description of the Pinecrest beds. Although potentially important material from the type locality in western Dade and eastern most Collier Counties, as well as from the Acline pits in Charlotte County, was not available, the author did manage to obtain material for study from Slough Ditch in the Brighton area of southern Highlands County (localities TU 520 and TU 752), from the vicinity of lock 65-D on the Kissimmee River in Highlands and Okeechobee Counties (TU 728, TU 769 and TU 770), and from the Mule Pen Quarry in Collier County (TU 1177). In all instances developmental profiles suggested an affinity with either Taxon B or Taxon C, which are considered herein to represent the same entity (quite possibly *S. evergladesensis)*. The absence of *S. floridanus* in these collections would suggest a correlation with the upper Pinecrest beds at APAC rather than the lower Pinecrest beds and Jackson Bluff Formation. Since all of these localities supposedly yielded a mixed Pinecrest/Caloosahatchee fauna, an alternative interpretation might be that all of the *Strombus* taken came from the Caloosahatchee components of those faunas. Given the ubiquitous nature of *Strombus* sensu stricto in the Pliocene and Pleistocene fossil record of southern Florida, this alternative seems less likely than the first.

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Abbreviations for institutions holding type material, figured specimens, and lots utilized in this study are:

CMNH - Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
HMNS - Houston Museum of Natural Science, Houston, Texas, USA
TU - Tulane University, New Orleans, Louisiana, USA
UF - Museum of Natural History, University of Florida, Gainesville, Florida, USA
USNM - U. S. National Museum of Natural History, Washington, DC, USA

VII. LOCALITY DATA

The following are Tulane University fossil locality numbers:

60. Jackson Bluff Fm., borrow pits at Jackson Bluff, Ochlockonee River (NW1/4 Sec. 21, T1S, R4W), Leon Co., Florida.
201. Bermont Fm., spoil banks at pit just south of Belle Glade (at Belle Glade Camp), Palm Beach Co., Florida.
520. Pinecrest beds, spoil banks, canal 0.9 mile east of Brighton on Florida Highway 70 (Sec. 25, T37S, R32E), Highlands Co., Florida.
539A. Bermont Fm., Shell Creek (upper beds), about 8 miles east of Cleveland (Sec. 30, T40S, R25E), Charlotte Co., Florida. (Designated as type locality of the Bermont Formation by DuBar, 1974, p. 221.)
580. Bermont Fm., North New River Canal spoil banks, 1 mile south of South Bay, Palm Beach Co., Florida.
728. Pinecrest beds, spoil banks on west side of Kissimmee Canal and east side of Kissimmee River, just across from U.S. Corps of Engineers Structure 65-D (Sec. 33, T36S, R33E), Okeechobee Co., Florida.
752. Pinecrest beds, spoil banks on south side of canal 41-C ("Slough Ditch") at crossing of county road, 4.3 miles east of Brighton and 1.4 miles south of Florida Highway 70 (SE1/4 Sec. 33, T37S, R33E), Highlands Co., Florida.
769. Pinecrest beds, spoil banks east side of Kissimmee River, 1 1/2 to 2 miles south of U.S. Corps of Engineers Structure 65-D (NE 1/4 Sec. 35, T36S, R33E), Okeechobee Co., Florida.
770. Pinecrest beds and Caloosahatchee Fm. mixed, spoil banks west side of Kissimmee River, 1 1/2 to 3 1/2 miles north of Florida Highway 70 (Secs. 10, 14, 15, and 28, T37S, R33E), Highlands Co., Florida.
797. Pinecrest beds, material exposed during construction of "Alligator Alley," 13.3 miles east of Florida Highway 29 (T49S, R32E), Collier Co., Florida.
978. Bermont Fm., spoil banks at pit on south side of waterworks, about 1 1/2 miles northeast of South Bay, Palm Beach Co., Florida.
991. Caloosahatchee Fm., Cochran rock pit, 2 1/2 miles west of La Belle, on north side of Florida Highway 80, Hendry Co., Florida.
1000. Pinecrest beds, APAC pits at east end of 17th street (T36S, R19E), about 8 miles east of U.S. Highway 301 at Sarasota (now northwest corner of Fruitville Road exit I-75), Sarasota Co., Florida.
1177. Pinecrest beds and Caloosahatchee Fm. mixed, Mule Pen Quarry, north side of Florida Highway 846, 9.1 miles east of U.S. 41 at Naples Park (SE1/4 Sec. 24, T48S, R26E), Collier Co., Florida.
1512. Caloosahatchee Fm. and Bermont Fm. mixed, De Soto Shell Company, pits 2 miles east of Florida Highway 31, about 12 miles south of Arcadia (T39S, R25E), De Soto Co., Florida.
1524. Pinecrest beds, Quality Aggregates Pit, off Richardson Road, north side of Fruitville Road and east of highway I-75, east of Sarasota, Sarasota Co., Florida.
1536. Pinecrest beds, Caloosahatchee Fm. and Bermont Fm. mixed, Star Ranch, Bergeron Rock Co. pit, 11.4 miles south of South Bay, and 0.8 mile west of U.S. Highway 27, Palm Beach Co., Florida.

The following are fossil collecting localities of the Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida:

GD003 Jackson Bluff Fm., Lake Talquin, Gadsden Co., Florida.
HI001 Bermont Fm., Leisey Shell Pit 01, bone bed, lower shell bed, and upper shell bed, Hillsborough Co., Florida (SE1/4, SW1/4 Sec. 15, T32S, R18E; Ruskin Quadrangle, USGS 7.5 minute series).
HI013 Bermont Fm., Leisey Shell Pit 03, bone bed, Hillsborough Co., Florida (N1/2 Sec. 15, T32S, R18E; Ruskin Quadrangle, USGS 7.5 minute series).

HI014 Ft. Thompson Fm., Leisey Shell Pit 03, upper shell bed, Hillsborough Co., Florida (N1/2 Sec. 15, T32S, R18E; Ruskin Quadrangle, USGS 7.5 minute series).

HI015 Bermont and Ft. Thompson Fms. mixed, Leisey Shell Pit 03, spoil, Hillsborough Co., Florida (N1/2 Sec. 15, T32S, R18E; Ruskin Quadrangle, USGS 7.5 minute series).

LN001 Jackson Bluff Fm., Jackson Bluff 01, material taken from borrow pit at power plant, Leon Co., Florida (NW1/4 Sec. 21, T1S, R4W; Bloxham Quadrangle, USGS 7.5 minute series).

LN002 Jackson Bluff Fm., Jackson Bluff 02, Leon Co., Florida (SW1/4 Sec. 16, T1S, R4W; Bloxham Quadrangle, USGS 7.5 minute series).

LN003 Jackson Bluff Fm., *Cancellaria* zone, Harvey Creek, Lake Talquin, Leon Co., Florida (SW1/4 Sec. 9, T1S, R3W; Bloxham Quadrangle, USGS 7.5 minute series).

LN004 Jackson Bluff Fm., Jackson Bluff, general, Leon Co., Florida (Sec. 16, 20, and 21, T1S, R4W; Bloxham Quadrangle, USGS 7.5 minute series).

The following are fossil localities collected by the author:

F01 Caloosahatchee Fm., Hendrickson Quarry, about .5 mile east of CR 768, just north of airport, Punta Gorda, Charlotte Co., Florida.

F07 Bermont Fm., spoil banks along the east sideof the North New River Canal, about 11 miles south of South Bay and just east of U.S. 27, Palm Beach Co., Florida.

F11 Ft. Thompson Fm., spoil from temporary excavation for new hospital, Bass Road near the intersection of SR 869, southwest of Ft. Myers, Lee Co., Florida.

F14 Ft. Thompson Fm., spoil piles along canal paralleling south side of new SR 80, 2.5 miles east of intersection with U.S. 441, northeast of Belle Glade, Palm Beach Co., Florida.

F15 Ft. Thompson Fm., spoil banks from ditch dug to depth of 4 to 5 meters, about 1/2 mile west of Burnt Store Road (CR 765) and 3 miles south of Charlotte County line, Lee Co., Florida. This locality is just to the north of FMNH site LE010, Burnt Store Road Pit 01A, (N1/2 Sec. 30, T43S, R23E; Matlacha Quadrangle, USGS 7.5 minute series).

The following are Recent collecting localities:

RFK01 Directly south of Key West, Florida; taken from stomachs of bat fish feeding among eel grass in 35-40 feet of water.

RFK02 Big Pine Key, Florida; Coupon Bight, off marker 3, Sheriff's Island, on sand in 3-6 feet of water.

RFK03 Hawk Channel, 3-4 miles south of Bahia Honda Key, Florida; 40 feet on soft mud bottom.

RFK04 East of Coffin's Patch, Marathon, Vaca Key, Florida; 32 feet on sand.

RFK05 Hawk Channel, off Duck Key, Marathon, Florida; 35 feet on sand.

RFG01 Off Beach Club Hotel, Naples, Florida; 8-10 feet on sand.

RFG02 San Carlos Bay, just west of Punta Ybel, Sanibel Island, Florida; 4-6 feet on sand.

RFG03 Gulf side, SanibelIsland, Florida; on intertidal sand bars 1 mile west of Punta Ybel.

RFG10 St. Andrews Bay at St. Andrews Recreation Area, Panama City, Florida; on grassy sand flats in 4-6 feet of water.

RTG01 Heald Bank, 31 miles ESE of Galveston, Texas; by divers in 12 fms. at Pleistocene rock outcrop, 2 miles south of #1 buoy. A lot of small juveniles from the Houston Museum of Natural Science (lot #15,249).

RCM01 Isla del Carmen, Campeche, Mexico; beach about 3 km west of Paso Real. (Close to Tulane locality R-52.)

RCM02 Sabancuy, Campeche, Mexico; beach at restaurant just south of where the road to Sabancuy meets Route 180.

RCM03 Punta Chanchec, 56 km NE of Isla Aguada, Campeche, Mexico. (= Tulane locality R-49.)

RCM04 Beach just south of Punta Sihoplaya, Campeche, Mexico.

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IX. ENDNOTES

[1] As Lyons (1991, p. 136) points out, the *North American Code of Stratigraphic Nomenclature* requires that lithostratigraphic units such as formations be differentiated in terms of lithologic characteristics. However, there are few lithologic criteria that can be used to separate the major biostratigraphic units in southern Florida that have been described over the years as formations. The author has decided to continue to utilize these long-standing formational names in this article because of their widespread use in the geological and paleontological literature and because of their potential for distinguishing chronologically distinct faunal units.

[2] These intermediate forms have generally all been equated with *S. pugilis* or *S. alatus* in broad-scale faunal studies (Heilprin, 1886, p. 83; Dall, 1890, p. 177; Olsson and Harbison, 1953, p. 273; DuBar, 1958, p. 214; and Hoerle, 1970, p. 63). Recently, however, Petuch has described two morphological variations purportedly found in the Bermont Formation as *Strombus evergladesensis* (1991, p. 14, pl. 1, figs. 11 and 12) and *Strombus lindae* (1991, p. 14, pl. 1, figs. 13 and 14). Therein and elsewhere (1992, p. 44) Petuch suggests that these two forms, together with *S. alatus*, represented three sympatric species, only one of which survived subsequent extinction events. This scenario of phyletic divergence and subsequent extinction used to explain morphological variation among early Pleistocene *Strombus* sensu stricto found in southern Florida excavations will be dealt with later in this paper.

[3] Some interesting examples of such computer-generated shell-forms can be seen in the introduction to the popular coffee-table shell book by M. G. Harasewych (1989, p. 17).

[4] The term "rate" as used here does not signify a measure of change **per unit of time,** but rather a measure of the change in a given measurement **per whorl.** It is in this sense that the term will be used throughout this study.

[5] For detailed locality data see Section VII.

[6] The presence of occasional specimens of *Vasum floridanum* McGinty, 1940, indicates the presence of Bermont material at the sites. On the other hand, the existence at the Florida Museum of Natural History of a single specimen of *Strombus hertweckorum* Petuch, 1991, from pit 1 suggests that an underlying Pinecrest fauna was uncovered on at least one occasion.

[7] When describing *S. alatus* in 1791, Gmelin referred to a figured specimen without shoulder spines on the body whorl (Martini, 1777, pl. 91, fig. 894). No type locality was given by him. This led to ongoing confusion regarding the identity of the taxon. Dall (1890) assumed that Gmelin's taxon was simply a spineless form of *S. pugilis*,

more prevalent in both the Recent and fossil record of Florida, but present throughout that species' range. Clench and Abbott (1941) maintained that the figured specimen referred to by Gmelin was the Florida form of *S. pugilis* (with or without spines on the body whorl) and, based on a number of distinguishing features, assigned a subspecific rank to it. Sanibel Island was designated as the type locality. Olsson and Harbison (1953), while retaining the subspecific rank in their work, suggested the re-elevation of *S. alatus* to full specific rank based upon the constant agreement of the Caloosahatchee form, referred to herein as Taxon C, with Gmelin's type figure. However, Morris (1951) had already taken this step based entirely upon the distinctions noted by Abbott and Clench, and Abbott himself soon followed suit (1954), thus presenting *S. alatus* as a distinct species in two of the most popular and authoritative American shell guides available in the early 1950's.

[8] As will be demonstrated later in this paper, it is only the lower portion of the Pinecrest beds (Units 5-10 at APAC) that correlate with the Jackson Bluff Formation. Whether these units are older than the *Cancellaria* zone of the Jackson Bluff Formation is also open to debate based upon the *Strombus* fauna. Although further study is required on this point when better-preserved material becomes available, the *S. floridanus* collected just below the lower *Vermicularia* bed (Unit 8) at APAC seem to show a greater affinity to the Jackson Bluff form of that taxon in some respects than to the form found in Units 6 and 7 at APAC.

[9] The horizontal line of a notched box plot indicates the median value for a sample and the notches approximate the 95% confidence interval for the sample median. McGill *et al.* (1978) have demonstrated that, in general, the difference in median values of two samples can be considered statistically significant if the notches do not overlap. However, they note that little confidence should be placed in "folded boxes" wherein the notch extends beyond the quartile box.

[10] It is possible to find *Strombus* specimens in spoil at the Quality Aggregates site that do have axial ribs or even weak shoulder knobs extending onto the body whorl. While some of the specimens are small enough to be confused with *S. floridanus* from the lower units of the pit, this form comes from the *Trochita* bed at the top of the section.

[11] Typically, once these specimens dry out the pattern is no longer visible to the naked eye.

[12] In a sample recently collected from spoil piles at the Florida Rock Quarry in western Dade County, made up at least in part of specimens which can be equated with the form identified by Petuch (1991) as *Strombus lindae*, 20% of the 42 adults exhibit axial sculpture on the body whorl. In at least two cases the sculpture consists of knobs indistinguishable in size and shape from those found on the body whorl of Recent *S. alatus*. The age of this material, however, has not been clearly established.

[13] The overlapping notches for the samples of *S. floridanus* and Taxon B, on the one hand, and for the samples of Taxon C and Taxon D, on the other, forces one to question the statistical significance of those pairs of sample medians. However, even if one were to equate the protoconch sizes of *S. floridanus* with Taxon B and Taxon C with Taxon D, there would remain a two-step incremental reduction over time. Larger data sets would be desirable to help resolve the nature of this change.

[14] It is often possible to collect more than one form from the same locality. However, this mixed material seems to be derived from spoil pile sampling. For the younger (*i.e.*, Bermont and post-Bermont) deposits found in the Everglades south of Lake Okeechobee this is the only strategy possible as the water table is at the surface and even borrow pits are flooded, being worked with drag lines. For the generally older deposits outside the Everglades northwest of Lake Okeechobee, where the water table is lower allowing borrow pits to be kept dry by pumping while being worked, *in situ* sampling does not yield a mixture of forms.

[15] The author has in his possession Recent *S. alatus* that have identical morphological characteristics, strong spiral sculpture on the body whorl combined with pronounced resting varices, and the same signs of predation. However, the collecting data are insufficient to allow conclusions to be drawn concerning the environmental conditions that might give rise to such morphological expressions.

[16] In an as-yet unpublished work Petuch will describe four more *Strombus* sensu stricto taxa from the Pliocene/Pleistocene of southern Florida. Although the type specimens have been studied, the author will await publication of the descriptions of the taxa and locality data before commenting.

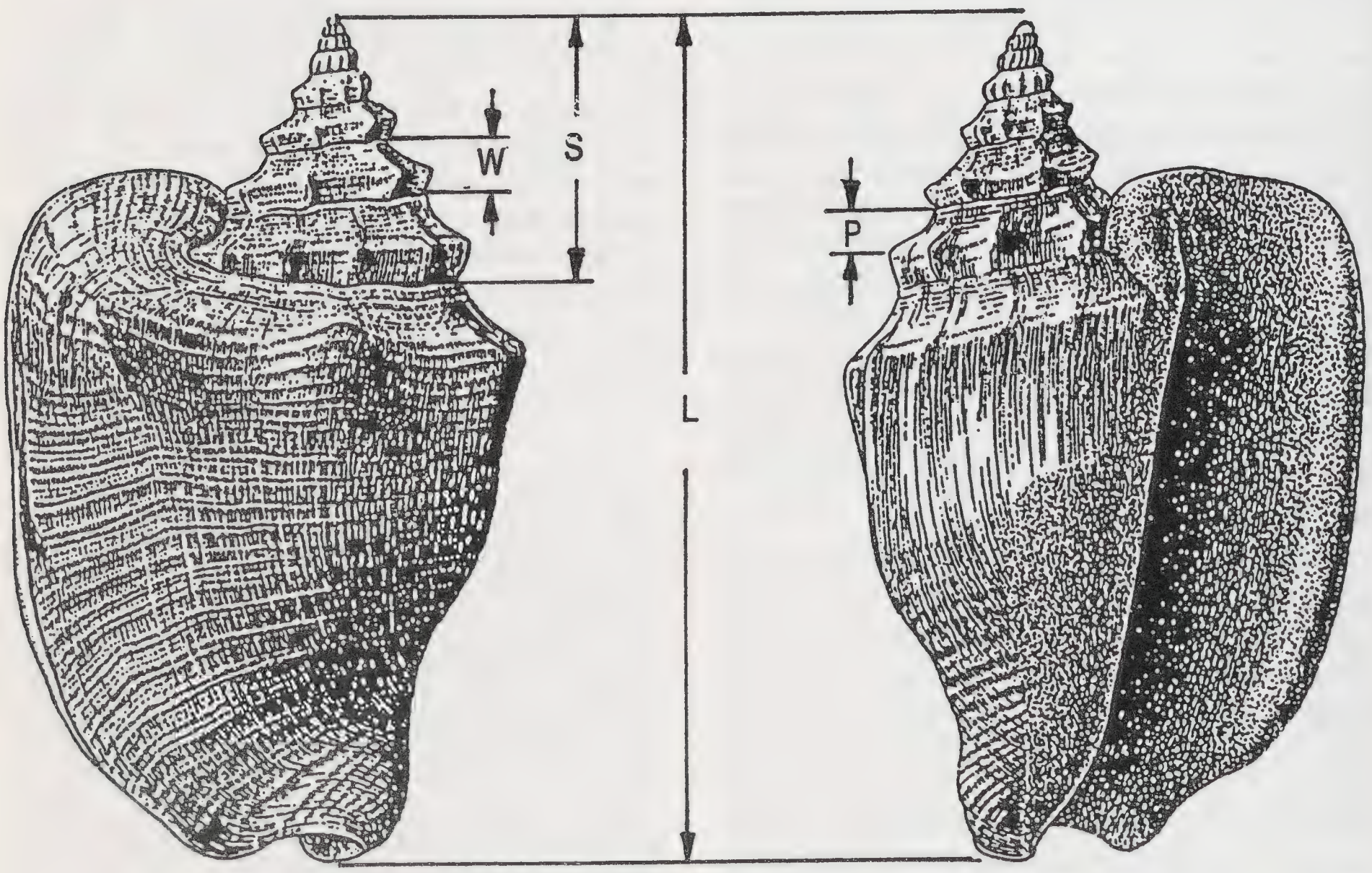
[17] Having studied thousands of specimens from the Miocene, Pliocene, Pleistocene, and Recent, this author finds it highly unlikely that any *Strombus* s.s. taxon yields adults smaller than about 45 mm.

[18] Interestingly, Petuch, in his popular work (1992, p. 43), includes a drawing of a "herd" of *S. evergladesensis* grazing on algal films in the Okeechobean Sea. All six of the specimens in the scene sport chevron patterns on the body whorl. Whether this represents artistic license on his part, based upon his having seen the pattern in older forms, or is an accurate reflection of the material collected from the type locality, is hard to say.

X. APPENDIX: MEASUREMENT PROTOCOLS

The following linear measures were made for all specimens analyzed. All measurements were carried out with vernier calipers, except as noted. For incomplete specimens, estimates were made of the amount of shell missing whenever possible. The letters in square brackets [ ] refer to Text-figure 20.

Shell length [L]. The distance from the apical tip to the anterior end of the siphonal



Text-figure 20. The linear measures carried out on those juvenile and adult *Strombus* analyzed in detail in this study. All measurements were made parallel to the axis of coiling using either vernier calipers, dividers and a millimeter scale, or a reticle mounted in the eyepiece of a binocular microscope.

canal, measured parallel to the axis of coiling.

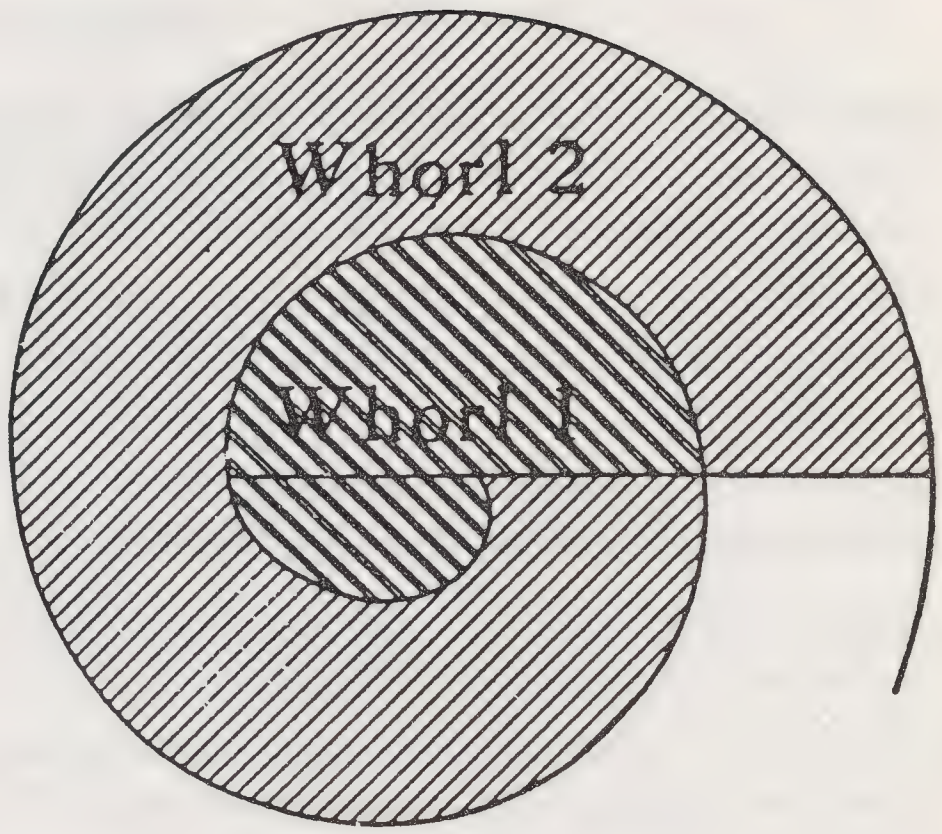
Maximum shell width. Measured perpendicular to the axis of coiling across the widest point of the shell (including the expanded lip in adults).

Dorsal/ventral body width. Measured in a direction that is both perpendicular to the axis of coiling and at right angles to the measurement of maximum shell width.

Spire height [S]. Measured parallel to the axis of coiling from the spire tip to the suture of the body whorl at the dorsal midline of adults (*i.e.*, roughly one quarter whorl before cessation of shell development in the expanded adult lip). For juvenile specimens, the distance measured was from the spire tip to the suture terminus. For very small specimens the measurement itself was performed under a binocular microscope fitted with a linear reticle scale. For larger specimens a divider and millimeter scale were used.

The following linear measurements were carried out for each spire whorl present. All measurements were made using a linear reticle scale mounted in the eye piece of an Olympus 7 to 40 power binocular microscope:

Whorl diameter. Specimens mounted so that the spire could be viewed from directly above. Those with intact protoconchs were oriented so that the initial whorls corresponded to Text-figure 21. With the whorls so defined, the diameter of each whorl present, defined as the distance from the mid-point to the end of the whorl, was measured. Incomplete specimens were oriented for analysis by setting the diameter of the smallest measurable whorl present equal to the mean value for that whorl as determined from measurements of perfect or more complete specimens in the sample. Once a specimen was oriented and the whorls thereby defined, the other two measurements and counts could be undertaken.



Text-figure 21. Shell orientation for the analysis of whorls (after Fisher *et al.*, 1964). Whorl diameter was measured from the mid-point to the end-point of a whorl at right angles to the axis of shell coiling.

Whorl height [W]. Specimens mounted so that the axis of coiling was oriented horizontally and the end points of the whorls facing upwards. Whorl height was determined by measuring the distance at the end of the whorl from the suture representing the point of attachment of that whorl (*i.e.*, the posterior suture) to the suture representing the point of attachment of the succeeding whorl (*i.e.*, the anterior suture).

Shoulder height [P]. Specimens mounted so that the axis of coiling was oriented horizontally and the end points of the whorls facing upwards. Shoulder height was defined as the distance measured at the end of the whorl from the posterior suture to the whorl periphery (for rounded whorls) or shoulder (for angled whorls).

(continued from p. viii)

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(continued on p. 152)

PRELIMINARY BIOSTRATIGRAPHY AND MOLLUSCAN FAUNA OF THE GOOSE CREEK LIMESTONE OF EASTERN SOUTH CAROLINA

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I. ABSTRACT

Despite 150 years of study, the stratigraphic relationship among Pliocene beds in South Carolina has not been clearly demonstrated. The Goose Creek Limestone and the closely related Raysor Marl have been particularly perplexing. Previously reported Goose Creek faunules have been too meager for effective comparison. Discoveries at the Martin Marietta Berkeley County Quarry and the Mason Dixon pit tripled the total number of documented species from the Goose Creek Limestone and provided a basis for correlating various literature records and Charleston Museum collections. The Goose Creek Limestone is divisible biostratigraphically into informal lower and upper units. These faunal units appear coincident with a lithic division, separated by an unconformity. The Raysor Marl unconformably overlies the lower Goose Creek Limestone, reversing the inferred stratigraphic sequence prevailing in current literature. Raysor Marl and upper Goose Creek Limestone faunules share numerous index taxa and appear to be laterally equivalent, coeval lithofacies. Both units are distinct from, and older than, the Duplin Formation at its Natural Well stratotype. The Bear Bluff Formation, at its stratotype locality, is lithically and faunally congruent with the upper Goose Creek Limestone.

II. INTRODUCTION

The Goose Creek Limestone is a moldic calcarenite of Pliocene age, originally described from Charleston, South Carolina (Tuomey, 1848; Sloan, 1907; Weems *et al.*, 1982). Its precise age and areal extent have been difficult to ascertain because of limited outcrops and sparse and disparate fossil assemblages. The present study is based on new localities in the Charleston area, in Berkeley County, and in Horry County, South Carolina. Limestone blocks from the Martin Marietta Berkeley Quarry and from the Mason Dixon pit south of Conway, South Carolina, are sufficiently indurated to preserve detailed molds, which were cast with latex to document the fauna. The Goose Creek Limestone is found in northeastern Georgia (Porter's Landing), eastern South Carolina, and southeastern North Carolina.

The Pliocene stratigraphy of the Carolinas is complex. Almost every stratigraphic unit discussed herein rests unconformably at some point on Eocene or Cretaceous bedrock. In contrast with the Virginia Yorktown, which is represented by laterally extensive beds exposed in bluffs of major rivers flowing across strike, the southern North Carolina and South Carolina Pliocene is represented by a patchwork of scour-and-fill deposits occasionally and ephemerally exposed by river cuts, sink

holes, marl pits, or quarries. Eventually, a stratigraphic consensus emerged, largely built on the work of C. Wythe Cook (1936) and Jules DuBar (see Oaks and DuBar, 1974; Campbell *et al.*, 1975; Ward, Bailey, and Carter, 1991; Owens, 1991). Our work challenges this consensus (Text-figure 1, column 1) at several points. As Pliocene stratigraphic patterns began to emerge in Virginia (L. Campbell, 1993), Georgia (Huddlestun, 1988) and Florida (Scott and Allmon, 1992), the South Carolina section required reexamination. Mapping around Charleston (Weems and Lemon, 1988; McCartan *et al.*, 1990) found numerous units that poorly fit the pattern. The stratigraphic model proposed here (Text-figure 1, column 2) challenges the supposed Pleistocene age of the Waccamaw, places the Goose Creek Limestone beneath the Raysor Marl, narrowly interprets the age of the Duplin based on the Natural Well stratotype, argues for a Duplin age younger than the Raysor and Goose Creek, and provides evidence for equating the Goose Creek Limestone and the stratotype section of the Bear Bluff Formation. Central to the argument is the first thorough documentation of the Goose Creek Limestone fauna.

This revision is based on field work done from 1986 to 1991. The senior author was responsible primarily for the field work, stratigraphy, faunal analysis, and casting the latex peels. The junior author assisted in logistics, statistical analysis, zoogeography, and systematics.

III. ACKNOWLEDGMENTS

We would like to thank our reviewers for suggestions that improved the manuscript. We also wish to express our appreciation to A. Sanders of the Charleston Museum and to Thomas Waller of the U.S. National Museum for permitting access to published and unpublished collections, and to Joseph Carter for the initial supply of latex. A South Carolina Academy of Sciences grant supported the field work. Daniel Cooke of the University of South Carolina at Spartanburg helped with the computer programming. Thanks also to those, too numerous to mention, who have shared locality information, specimens, and other support during the various phases of this study.

IV. METHODS AND MATERIALS

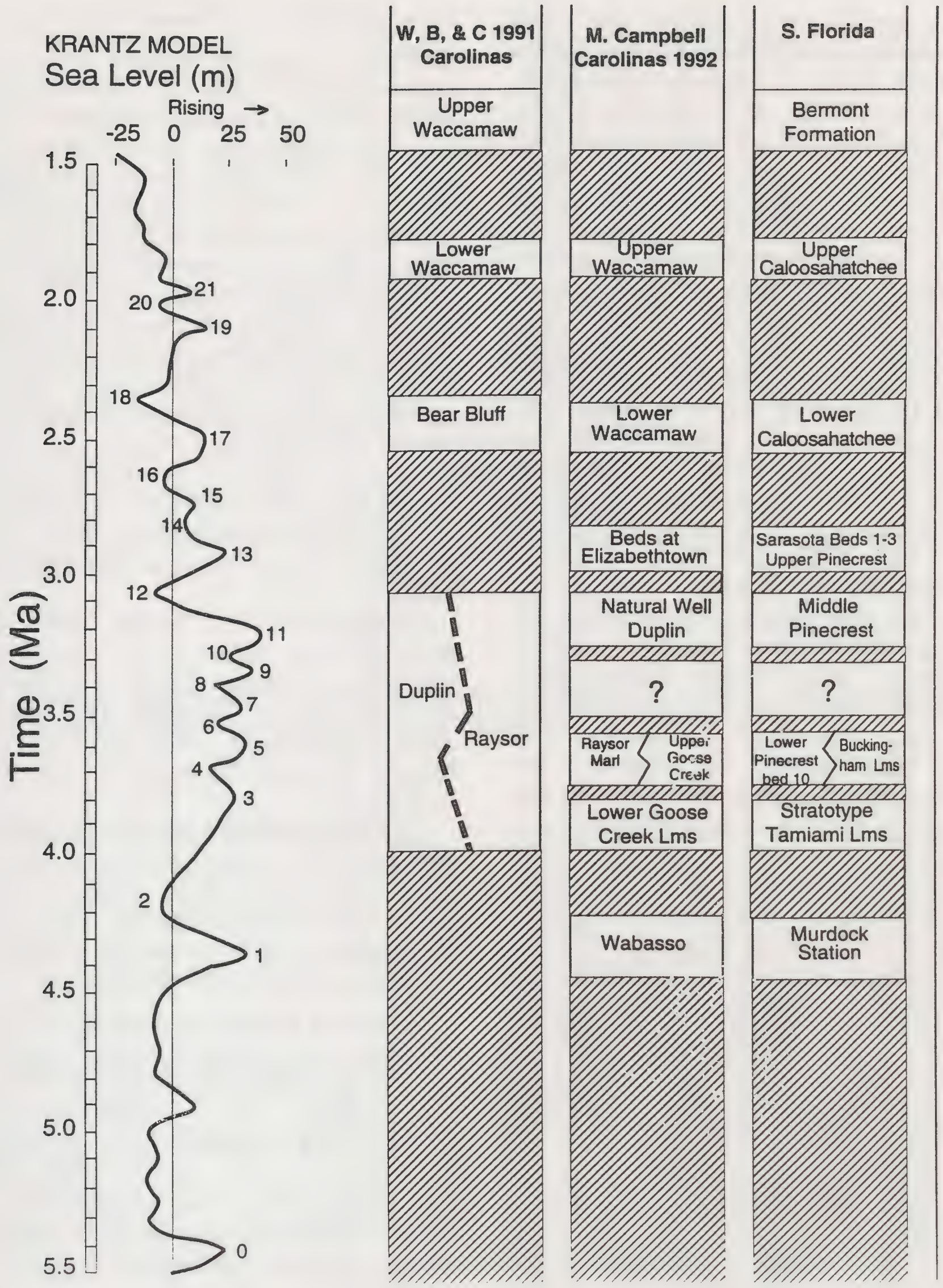
Latex Casting

The Goose Creek Limestone is a leached, moldic limestone that once contained an abundance of molluscs and other invertebrates. Where soft, the calcarenite preserves few fossils, but several new localities preserve a more indurated lithology with good to exquisitely detailed molds. These were cast with liquid latex. The faunal listing (Appendix II) was based on over 700 individual castings. An illustrated systematic catalog is planned.

Database and Statistical Methods

We have attempted to place Carolinian Pliocene units in a biostratigraphical context by comparison with a comprehensive database consisting of distribution data for 1127 molluscan species from approximately 180 Pliocene localities in Virginia and the Carolinas. The species list in Appendix II is the Goose Creek subset of the larger data base. Appendix I lists localities and literature sources for 19 Goose Creek Limestone sites, plus data on Duplin, Raysor; and Tamiami sites for comparison. Statistical analysis of the Virginia portion of the data has been published (L. Campbell, 1993); analysis of the complete data set is in progress.

Dice similarity coefficients and percentages-held-in-common were used for statistical analysis (Table 2; Appendix I). The Dice coefficient also is known as the Sorensen coefficient (Sneath and Sokal, 1973; Pielou, 1984). It is one of the best coefficients for representing sparse data sets (Archer and Maples, 1987; Maples and Archer, 1988), and has demonstrated utility in distributional analysis of ostracodes (Hazel, 1971) and of molluscan populations (Leal and Bouchet, 1991; Leal, 1991). The Dice similarity formula is $2C/(A + B)$, where A is the total number of species from one locality, B is the total number of species from a second locality, and C is the number of species in common between the two localities. An alternative formula is $Dice = 2A/(2A + B + C)$ in which A = the number of species in common, B and C are the number of single occurrences in the two populations being compared. Dice values may be expressed with the multiplier, "x 100," but this is not used in this study.



Text-figure 1. Correlation chart comparing the Krantz Oxygen Isotope model with Pliocene stratigraphy of southeastern North Carolina and South Carolina (M. Campbell, 1992), and of southern Florida. Comparison also is made with the stratigraphic model of Ward, Bailey, and Carter (1991), and with southern Florida. The stratigraphy of southern Florida is taken from Scott and Allmon (1992) and Lyons (1991). The South Carolina and southern Florida correlations with the Krantz curve are our interpretations. The chronostratigraphic placement of the Ward, Bailey, and Carter model is based on their age assignments *and is not intended to show parallel correlations*. For example, the Ward, Bailey, and Carter model places the lower Waccamaw beds at the K-19-21 level, our model places the upper Waccamaw at this level. We are not cross-correlating these units, but rather pointing out the differences in age interpretations.

The Dice coefficient relates to the more familiar Jaccard coefficient by the algebraic identity, Dice = Jaccard value x 2/(1 + Jaccard value) and is, therefore, "monotonic with and always greater than or equal to the Jaccard coefficient" (Sepkoski, 1974, p. 2). Dice coefficients are a comparative statistic only. They provide high values when there is a small range of data values, when the two populations being compared are equally diverse, and when the commonality is high. Lower Dice values result from partial and incomplete data sets. In one study, unity values among samples taken from the same stratum in a single outcrop fell between Dice values of 0.700 and 0.800 for a sequence of mollusc-rich beds in the Yorktown Formation (L. Campbell, 1976). The Dice values for the Recent and the Miocene are not exactly comparable with the remaining matrix because the distributional data contains only overlap occurrences rather than documenting the entire Recent and Miocene faunas. Therefore, for Recent and Miocene Dice values, "A" remains the comparison locality, and "C" remains the commonality, but the value of "B" is the sum of all Pliocene species extending into the Recent or originating in the Miocene. The Dice values for the Recent and Miocene are not equivalent conceptually with the remaining comparisons. To emphasize the limitation, the first and last columns in the statistical matricies are coded "ALSO RECENT" and "ALSO MIOCENE." This limitation does not apply to percentage data in which the Miocene or Recent totals are irrelevant.

Such percent-in-common statistics have been called the Simpson coefficient (Sneath and Sokal, 1973), when they are calculated as commonality divided by the smaller of the two populations being compared. We differ by calculating the percentage for the population in consideration, whether it be larger or smaller than the population being compared. Ward and Gilinsky (1993) have questioned such use of "Lyellian faunal percentages" by L. Campbell (1993). Lyellian percentages reference the Recent only. Percentage-in-common with the Recent is one of eight biostratigraphic comparisons calculated in our analysis.

Concept of Faunal Standards

Widely disparate species richness data are awkward to analyze. Incomplete distribution, habitat changes between outcrops, varied taphonomies, and variable collecting effort all contribute to the disparity. However, uniting a set of unequivocally contemporaneous faunules into a standard fauna can reduce some of the randomizing effects inherent within comparisons of individual localities. Such composite faunas become standards against which more variable or equivocal assemblages may be examined. For the Pliocene of southeastern North Carolina and South Carolina, six composite standard faunas were determined from their high Dice similarity levels and shared index species. The faunules compiled to produce the standard faunas were:

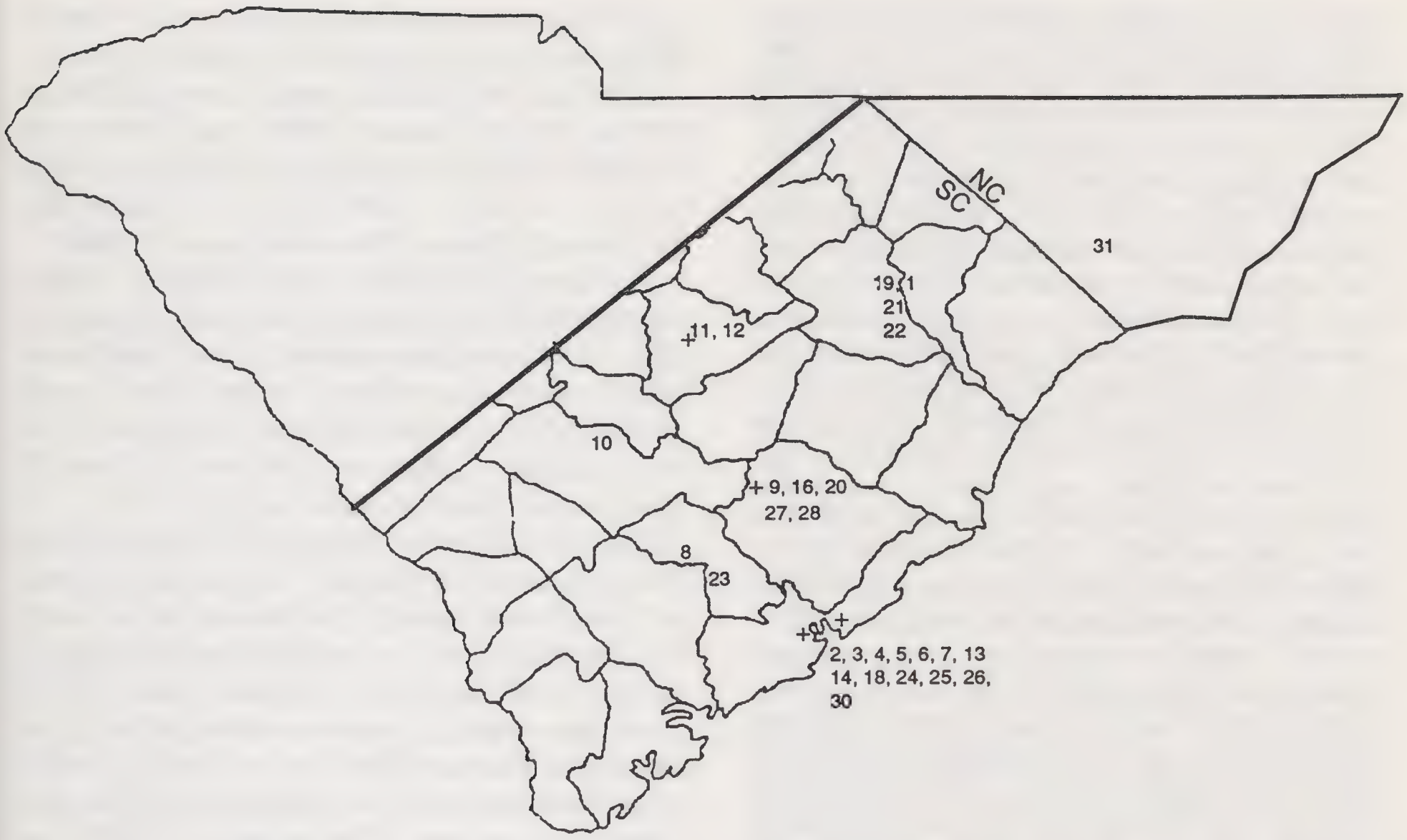
LOWER GOOSE CREEK LIMESTONE STANDARD, sum of 3 localities: the stratotype at Goose Creek and the Grove Plantation (both Tuomey, 1848); and the aragonite-leached Pliocene bed at the Martin Marietta Berkeley Quarry (USCS collections).

UPPER GOOSE CREEK LIMESTONE STANDARD, sum of 4 localities: Giles Bluff (Tuomey, 1848); plus the Mason Dixon pit, G & C Mining Co. pit, and Thompkins pit, all in the Conway, South Carolina, area (USCS collections).

RAYSOR MARL STANDARD, sum of 3 localities: the original Raysor material in the Sloan collection (Ward and Huddlestun, 1988); the aragonite-preserved faunule at the Martin Marietta Berkeley Quarry near Cross, South Carolina (Ward and Huddlestun, 1988; Campbell *et al.*, 1975; USCS collections); and the *Chama* beds at Lynchburg, South Carolina (USCS collections).

STRATOTYPE DUPLIN STANDARD, sum of 3 localities: Natural Well (Campbell, Campbell, and Carter, 1994, this volume); Muldrow Place (Gardner and Aldrich, 1919); and Tearcoat Branch (S. Campbell, 1974; and in preparation).

LOWER WACCAMAW STANDARD, sum of 3 localities: the lower beds at Calabash; the lower beds at Windy Hill, South Carolina; and the faunule at Old Dock, North Carolina.



Text-figure 2. Distribution of Goose Creek Limestone localities in North and South Carolina. Locality numbers refer to the localities listed in Appendix I.

UPPER WACCAMAW STANDARD, sum of 12 localities: mostly from DuBar, plus faunules from the Waccamaw lectostratotype of Blackwelder (1979), Dall (1892), USCS collections; and the upper beds at Calabash, North Carolina (USCS collections).

V. DISCUSSION OF STRATIGRAPHY

Described Pliocene Formations of Eastern South Carolina

Current literature cites at least seven formations of Pliocene age from South Carolina, but application of these units continues to be problematical. A summary of the various formations and their use follows. Although the Pliocene is formally subdivided into upper and lower units, an informal "mid-" or "middle" Pliocene continues to be a useful concept (*e.g.*, Behrednt and Cooper, 1991). Dowsett and Cronin (1990) define middle Pliocene as 3.5 to 2.5 Ma. We use mid-Pliocene to indicate those strata younger than the Wabasso and older than the lower Waccamaw, *i.e.*, between 3.9 and 2.5 Ma.

(1) *Wabasso Beds*

The "Wabasso" formation is an informally named stratigraphic unit (Huddlestun, 1988, p. 98) of early Pliocene subsurface deposits extending from southeastern South Carolina to Florida. The sediments are calcareous, phosphatic, and probably preserve calcitic shell only. Unusually large specimens of *Chesapecten jeffersonius* (indicative of Pliocene-aged deposits; Ward and Blackwelder, 1975) were found by SCUBA divers in probable Wabasso beds at the bottom of the Savannah River. The specimens were on display at the 1988 South Carolina fossil fair, and remain in the possession of their collectors. The age of the Wabasso, based upon planktic foraminifera is zone N-18, or PL-1, between 4.5 and 5.0 Ma (Huddlestun, 1988, p. 100).

(2) *Goose Creek Limestone*

Weems *et al.* (1982, p. H140) characterized this unit as follows:

> "In the Charleston area, the Goose Creek Limestone . . . is a medium to coarse-grained, quartzose and phosphatic, sparsely shelly,

pale buff-gray (wet) to chalk white (dry) calcarenite. Shell material was once abundant, but aragonitic forms have been extensively leached, leaving only molds and casts. It contains kaolinite in the greater than 2 micron-size fraction and both kaolinite and illite-smectite in the less than 2 micron-size fraction. Locally its composition is influenced by the nature of the substrate. For example, near Mount Holly, a channel containing Goose Creek Limestone is incised deeply into the Eocene Parkers Ferry Member of the Cooper Formation (Ward *et al.*, 1979); there the Goose Creek is nearly a calcilutite, like the Parkers Ferry, and contains calcilutite clasts obviously derived from the subjacent and adjacent beds of the Parkers Ferry. Where the Goose Creek Limestone lies on the Oligocene Ashley Member of the Cooper Formation, which is a compact, quartzose and phosphatic, fine-grained calcarenite, it is similar to that lithology, though coarser grained, much less dense, and light-buff-gray rather than olive-brown. Locally, in the Charleston area, the distribution of the Goose Creek is well known . . . Except for five localities, however, it is known only from auger holes."

Weems and Lemon (1988) mapped the Goose Creek Limestone within an approximate radius of 80 km around Charleston.

(3) *Duplin Formation and Raysor Marl*

The Duplin Formation was described by Dall (1898b, p. 338) for beds at Natural Well, a sink hole in Duplin County, North Carolina. Huddle (1940, p. 227) restricted the Duplin to the top meter of Dall's type section. Much confusion exists over the interpretation of the Duplin. The question essentially centers on whether to interpret the unit narrowly in strict terms of its stratotype section, or broadly, to include several transgressive-regressive sequences. At the stratotype locality, the Duplin sediments consist of quartz sand with abundant, well-preserved aragonitic shells. The fauna of the Natural Well stratotype has been published piecemeal by Conrad (1841), Dall (1890-1903), Mansfield (1930-1932), Gardner (1944, 1948), and others. However, the majority of species recorded by Dall (1903) from "Natural Well and vicinity of Magnolia" came from the Strickland Farm rather than from Natural Well (Campbell, Campbell, and Carter, this volume). S. Campbell (1974) published a listing of the fossils and index species from the Natural Well-equivalent Tearcoat Branch locality in Sumter County, South Carolina, and demonstrated an age of zone N-20, or about 3.0 to 3.5 Ma for that site.

The Raysor Marl, as described by Sloan (1907a, 1907b), Cooke (1936), and Weems *et al.* (1982), is a silty quartz sand. The original type locality near Raysor's Bridge on the Edisto River, has not been rediscovered and probably lies buried under slumped stream bank deposits (Pooser, 1965). Lithostratigraphically and biostratigraphically equivalent, silty sand and aragonite-preserved shell beds are present at the Martin Marietta Berkeley Quarry near Cross, South Carolina.

Blackwelder and Ward (1979) described the "Raysor Formation" as a calcareous sediment containing shells, and redefined the formation in terms of a neostratotype section at Givhans Ferry State Park. However, the neostratotype section is not typical of the Raysor Marl, *sensu* Sloan (1907), but is lithically conformable with the Goose Creek Limestone (Weems *et al.*, 1982, p. H142-144). The Givhans bluffs site also provides the informal stratotype section of the "Givhans Beds" of McCartan (1990). Weems *et al.* (1982) argued for abandoning the Givhans Ferry neostratotype for the Raysor Marl. Ward and Huddlestun (1988) illustrated the Raysor macrofauna from Sloan collection specimens, and documented a substantial planktic foraminiferal faunule from matrix removed from Sloan specimens. These yielded an age of zone N-20 or PL-3.

(4) *Bear Bluff Formation*

According to McCartan (1990, p. 3), "The oldest known horizons of the Goose Creek are possibly slightly older than the oldest known horizons of the Bear Bluff (Bybell, 1990), but poor preservation of most fossils in both the Goose Creek Limestone and the Bear Bluff Formation precludes firm relative stratigraphic placement of these two units at present."

The Bear Bluff Formation was described by DuBar *et al.* (1974, p. 156) with a stratotype section at Bear Bluff on the Waccamaw River, north of Conway, South Carolina. DuBar *et al.* (1974) ascribed to the Bear Bluff a number of lithologies, including basal limestone at the stratotype and at Lake Waccamaw, North Carolina, and upper unconsolidated sand with an abundant, aragonite-preserved molluscan

fauna at other localities. Ward and Gilinsky (1993) assert that a well-preserved assemblage at Elizabethtown, North Carolina, is the nearshore, lateral equivalent of the leached calcarenites at the Bear Bluff stratotype.

The stratotype section consists only of DuBar's lower unit, a moldic comminuted shell calcarenite capped by unfossiliferous sand and soil. Numerous studies have suggested a late Pliocene age (zone N-21) for the upper unit (Cronin *et al.*, 1984). However, no previous study apparently has documented macrofauna from the stratotype section of the Bear Bluff Formation. Appendix II (locality 105) records 27 species from the Bear Bluff stratotype, including 19 wide ranging species found in Waccamaw, Duplin, Raysor Marl, and upper Goose Creek faunas; seven species restricted to the Duplin, Raysor Marl, and upper Goose Creek faunas; and one variety, *Carolinapecten eboreus* var. *walkerensis*, uniquely restricted to the upper Goose Creek fauna. The latter taxon, a warped scallop shell exceeding 200 mm in maximum diameter, is abundant at nearby Conway area pits including the G & C mining company, the Mason Dixon pit, and the Tompkins Quarry (see Appendix I). These correlative localities contain calcarenites with far richer faunules, including such age-indicative taxa as *Ecphora quadricostata*, *Ecphora bradleyae*, *Chesapecten septenarius*, *Glycymeris americana* var. *abberans*, *Pecten brouweri*, and *Encope macrophora*, most of which are pre-Duplin (*sensu* Natural Well) species (Tables 1 and 3).

Carbonate percentages from the leached calcarenite sediments of the Bear Bluff stratotype are similar to those of the Goose Creek Limestone (M. Campbell, in preparation), and the faunule (locality 105, Appendices I and II) is compatible with that of the Mark Clark pit and the Seaboard Railroad ditch (localities 13 and 14) in Charleston. Therefore, the Bear Bluff stratotype is pre-Natural Well Duplin in age, lithically and faunally equivalent with the upper Goose Creek Limestone. The remaining, upper Bear Bluff units of DuBar *et al.*

	DUPLIN SANDS	RAYSOR SANDS	GOOSE CREEK UPPER BED	LIMESTONE LOWER BED
Barbatia leonensis	r	x	x	
Glycymeris americana abberans		x	x	r
Pecten hemicyclicus		r	r	x
Pecten brouweri			x	
Leptopecten leonensis		r	r	x
Carolinapecten eboreus walkerensis		x	x	
Chesapecten septenarius		x	x	x
Chesapecten madisonius ssp.			r	r
Chesapecten jeffersonius				x
Nodipecten collierensis				x
Nodipecten peedeensis			x	
Placunanomia plicata (typical form)	x		x	x
Placunanomia burnsi				x
Spondylus n.sp.	r		r	r
Hyotissa haitensis			x	x
Diplodonta subvexa			x	
Malea sp. cf. M. densecostata			r	
Ecphora bradleyae	r		x	
Terebraspira elegans	r		r	
Encope macrophora			r	x

Table 1. Molluscan and echinoid index species of the lower and upper zones of the Goose Creek Limestone. Detailed locality and distribution data in Appendices I and II. X = common r = rare.

(1974) contain a Waccamaw-equivalent, post-Duplin macrofauna (Campbell *et al.*, 1975) and ostracode fauna (lower *Puriana mesocostalis* zone; Hazel and Cronin, 1979). Multi-transgressional formations are valid, and common in the Atlantic Coastal Plain (Huddlestun, 1988). However, if a proposed formation contains members older and younger than beds of another well-defined formation in the same region,

PERCENT IN COMMON

	R	UW	LW	E	D	RA	UGC	LGC	W	M	
R	-	48.2	38.6	33.8	21.1	21.1	20.0	22.7	-	-	R
UW		-	75.6	67.7	49.1	25.6	19.3	12.5	-	10.1	UW
LW			-	66.1	45.4	23.1	17.2	11.5	-	7.6	LW
E				-	64.5	40.3	37.1	24.2	-	14.5	E
D					-	39.1	30.5	20.1	-	12.5	D
RA						-	53.1	36.4	-	27.3	RA
UGC							-	51.7	-	25.3	UGC
LGC								-	-	28.6	LGC
W									-	-	W
M										-	M

% calculations based on the number (N) of the younger of the two units compared

DICE SIMILARITY COEFFICIENTS

	R	UW	LW	E	D	RA	UGC	LGC	W	M	
R	-	.540	.468	----	.265	.186	.167	.141	-	-	R
UW		-	.684	.211	.418	.316	.253	.185	-	.212	UW
LW			-	.175	.430	.305	.239	.179	-	.183	LW
E				-	.155	.184	.192	.166	-	----	E
D					-	.535	.437	.318	-	.267	D
RA						-	.574	.463	-	.360	RA
UGC							-	.620	-	.315	UGC
LGC								-	-	.300	LGC
W									-	-	W
M										-	M

R = ALSO RECENT N = SPECIES RICHNESS
UW = UPPER WACCAMAW N = 336 molluscan species
LW = LOWER WACCAMAW N = 407
E = ELIZABETHTOWN BEDS N = 62
D = STRATOTYPE DUPLIN AND EQUIVALENTS N - 453
RA = STRATOTYPE RAYSOR AND EQUIVALENTS N = 209
UGC = UPPER GOOSE CREEK N = 178, Calcitic an moldic preservation
LGC = LOWER GOOSE CREEK N = 119, Calcitic and moldic preservation
W = WABASSO N = 2 Number too small for meaningful comparison
M = ALSO MIOCENE

Table 2. Percentage and Dice Similarity Coefficient matrices for Pliocene faunas of southern North Carolina and South Carolina.

yet excludes the other formation, then the proposed formation becomes discoherent and should be abandoned.

(5) *Waccamaw and Cypresshead Formations*

The Waccamaw Formation was described from the Waccamaw River, South Carolina, by Dall (1892, p. 209). Blackwelder (1979, p. 54) proposed a lectostratotype section at the Tilly Lake outcrop (Waccamaw River, South Carolina). Aragonitic shell preservation is typical. The catalog by L. Campbell *et al.* (1975, "WA-"

CAROLINA PLIOCENE INDEX SPECIES

a. *Placopecten clintonius (at Aurora, NC)*
b. *Chesapecten jeffersonius*
c. *Placunanomia burnsi*
d. *Chesapecten madisonius 10-14 rib average*
e. *Chlymys decemnarius*
f. *Nodipecten collierensis*
g. *Nodipecten peedeensis*
h. *Ecphora bradleyae,*
i. *Chesapecten septenarius*
j. *Encope macrophora*
k. *Anadara propatula*
l. *Striarca centenaria*
m. *Glycymeris americana abberans*
n. *Hemimetis magnoliana*
o. *Ecphora quadricostata*
p. *Plioptygma carolinensis*
q. *Coralliophila leonensis*
r. *Pecten holmesi*
s. *Stralopecten ernestsmithi*
t. *Scaphella precursor*
u. *Carolinapecten eboreus senescens*
v. *Argopecten vicenarius*
w. *Abra aequalis*
x. *Mulinia lateralis*
y. *Crassostrea virginica*
z. *Carolinapecten solaroides*

Table 3. Range zones of 27 Pliocene molluscan and echinoid index species from the Carolinas.

localities, especially "WA-4") contains the most thorough published listing of Waccamaw Formation molluscs (*sensu* Dall, 1892). Beds with Waccamaw-related faunas older than the stratotype section have been called the "shelly facies of the Bear Bluff Formation" by DuBar *et al.* (1974), but were included in Waccamaw by Campbell *et al.* (1975). The Waccamaw Formation contains planktic foraminiferal zone N-22, latest Pliocene to earliest Pleistocene age (Cronin *et al.*, 1984, p. 31).

The Cypresshead Formation was described by Huddlestun (1988, p. 119) for a complex of mostly subsurface Pliocene sands and clays previously ascribed to a number of different formations in South Carolina, Georgia, and Florida. Huddlestun (1988, p. 122) mapped the Cypresshead as far north as Summerville, South Carolina, where it is applied to the same beds mapped as Waccamaw by DuBar *et al.* (1974, p. 158) and Penholoway by Richards (1943), Colquhoun *et al.*, (1968), and Weems and Lemon (1988). Sediments are typically quartz sands and clay beds with rare deposits of marine shells. The shells, when present, show aragonitic preservation. A sparse microfauna of planktic and benthic foraminifera was described by Huddlestun (1988, p. 124). The ages of the Cypresshead Formation are Pliocene (N-21 or PL-5, Huddlestun, 1988), and lower Pleistocene (Corrado *et al.*, 1986; Bybell, 1990) for the "Penholoway" beds. Use of the Cypresshead Formation for the Charleston area follows Huddlestun (1988).

Age, Faunal Character, and Stratigraphic Placement of the Goose Creek Limestone

Age-indicative species from the Goose Creek stratotype were listed by Tuomey (1848), Cooke (1936), and by Weems *et al.* (1982). Tuomey (1848, p. 179) reported 15 calcitic and moldic species, including *Siphocypraea carolinensis*, *Encope macrophora*, *Hemimetis magnoliana* (as *Tellina biplicata*), *Amusium mortoni*, *Pecten hemicyclicus*, *Panopea reflexa*, and *Spondylus* species. Cooke (1936, p. 129) cited 11 species, including *Pecten hemicyclicus*, *Amusium mortoni*, and *Encope macrophora*. Weems *et al.* (1982, fig. 32) cited *Amusium mortoni* and *Argopecten eboreus* and the calcareous nannofossils *Reticulofenestra pseudoumbilica* (Gartner, 1967) and *Sphenolithus abies* Deflandre, 1954. Of these, *Siphocypraea carolinensis*, *Hemimetis magnoliana*, and *Panopaea reflexa* became extinct at the end of the time of Duplin deposition. *Encope macrophora*, *Pecten hemicyclicus*, and *Spondylus* are common in the lower Goose Creek Limestone, but rare and isolated in the upper Goose Creek Limestone and the Raysor Marl (Table 1). Based on nannofossils, Weems *et al.* (1982, p. H142) concluded "these fossil data imply that the Goose Creek Limestone is early to middle Pliocene (between 5 m.y. and 3 m.y.) in age."

Nearby Goose Creek calcarenite deposits at Yeaman's Hall and at Fetteressa (Appendix I, locality 14) (Seaboard Railroad ditch of Weems *et al.*, 1982) added additional elements including *Nodipecten peedeensis* and *Chesapecten septenarius*, both of which became extinct prior to deposition of the Duplin. The co-ocurrence of common *Chesapecten septenarius*, *Pecten hemicyclicus*, *Spondylus* sp., and *Encope macrophora* in the Pliocene calcarenite at the Martin Marietta Berkeley Quarry provided the basis for correlation with the faunule of the Goose Creek stratotype. *Nodipecten peedeensis* and *Chesapecten septenarius*, along with rare *Pecten hemicyclicus* and *Encope macrophora*, provided the basis for correlation with the calcarenites around Conway, South Carolina.

Determining a Goose Creek fauna from existing literature is complicated. Calcitic echinoids, pectinids, and oysters are commonly preserved but often difficult to extract from adhering matrix. The aragonitic species are either completely eliminated or preserved as molds. A literature search yielded a total of 74 species of Pliocene macro-invertebrates reported from mid-Pliocene calcarenites around Charleston and on the Pee Dee River (localities and authors in Appendix I). But a maximum of 18 species per locality and disparate assemblages suggest no obvious biostratigraphic reason for uniting them. Recently discovered Goose Creek faunules at the Martin Marietta Berkeley Quarry, and around Conway, South Carolina, preserve both a rich and abundant calcitic fauna and a diverse moldic assemblage from which latex peels were taken. The seemingly disparate faunules, including that of the stratotype at Goose Creek, are shown

herein to be compatible subsets of these larger assemblages (Appendix I). Appendix II lists the distribution of approximately 250 Goose Creek macrofossil species now documentable in the Charleston Museum, the U.S. National Museum, or the USC Spartanburg collections. Additional age determinations for the Goose Creek Limestone include foraminiferal zone PL-3 (Ward and Huddlestun, 1988, p. 73), and 3.9 to 3.2 Ma, or Zone NN 15 to mid-NN 14 (Bybell, 1990).

The discovery of the Raysor Marl unconformably overlying the lower Goose Creek Limestone in the section at the Martin Marietta Berkeley Quarry contradicts the widely held opinion in literature that the Goose Creek Limestone is younger than the Duplin. The relative ages have been reversed for at least two reasons. The first problem arose with the inclusion of a relatively rich faunule of 27 molluscan species that Tuomey and Holmes (1855-1857) reported from the George H. Smith property on Goose Creek near the stratotype, a locality they called "Smith's, Goose Creek" (Appendix I, locality 7). This site has not been located with certainty, but is generally associated with Yeaman's Hall. From this site, Tuomey and Holmes reported both typically moldic Goose Creek Limestone taxa and an aragonite-preserved faunule containing several Waccamaw index species, including *Pecten holmesi* Dall, 1898 (= *Janira affinis* Tuomey and Holmes, 1855). This shelly unit belongs to the Cypresshead Formation, and should be excluded from the concept of the Goose Creek Limestone.

The influence of the "Smith's, Goose Creek" faunule on subsequent age interpretations of the Goose Creek Limestone cannot be measured because it was rarely cited. However, most subsequent authors have estimated Goose Creek ages compatible with the "Smith's" faunule rather than with those of the calcarenite localities.

The second error came from the correlation of the Goose Creek Limestone and the Tamiami Limestone (Cooke, 1936), based on the common occurrence of *Encope macrophora*. Although that faunal equivalency can now be reinforced with numerous additional co-occurrences (see Systematics), and is reasonably established, Cooke (1936) further believed the Tamiami Limestone to be a member of the Caloosahatchee Formation and, therefore, Waccamaw-equivalent. The relative placement of the Tamiami Limestone in southern Florida was rectified by Olsson and Petit (1964), but the correction was not extended into the Carolinas.

Lithostratigraphic and Biostratigraphic Subdivision of the Goose Creek Limestone

Moldic calcarenite rocks were exposed in the now flooded Mason Dixon Company pit located just east of U.S. Rt. 701, approximately two km south of Conway, Horry County, South Carolina. Rocks of this pit correlated with the Goose Creek Limestone in Charleston and at the Berkeley Quarry, based on carbonate percentages (M. Campbell, in preparation), index species (Appendix II), and a high Dice similarity index (0.516) (Appendix I). Based on these commonalities, the Mason Dixon beds were assigned to the Goose Creek Limestone (M. Campbell, 1990), the first recognition of that formation in Horry County. However, the faunal statistics (Appendix I) for the Mason Dixon pit also indicated a stronger affinity with the mid-Pliocene Duplin Formation and Raysor Marl faunas. In contrast, the Berkeley Quarry faunule showed stronger affinities for the lower Pliocene and upper Miocene faunas.

A reevaluation of the faunules of all reported sites in the Charleston area and Horry County revealed related, but biostratigraphically distinct, assemblages (Tables 1 and 2). Weems (1989, personal communication) found an unconformity within the Goose Creek Limestone in cores near Charleston, dividing the unit into upper and lower units. The Mason Dixon beds and the Berkeley Quarry beds and their respective equivalents probably conform with the upper and lower lithostratigraphic divisions. At the Martin Marietta Berkeley Quarry, the upper Goose Creek-equivalent Raysor Marl is separated from the subjacent lower Goose Creek calcarenite by an erosional, pebble bed unconformity (M. Campbell, in preparation). However, no exposed calcarenite section known to us preserves either the unconformity or the two zones. The upper and lower calcarenites are not separable lithically, and many outcrops and core samples do not contain the index species necessary to

separate them. Therefore, both units should be referred to the Goose Creek Limestone. Where faunules are sufficiently rich, the two units may be distinguished biostratigraphically by index species as shown in Table 1 and Appendix II.

All Conway area and Horry County mid-Pliocene calcarentites, including the stratotype of the "Bear Bluff Formation," belong to the upper Goose Creek Limestone. Upper Goose Creek localities in the Charleston area include Feteressa, the Seaboard Railroad ditch, and the Mark Clark Expressway pit. The Berkeley Quarry, the Givhans Ferry section, and a number of Charleston localities, including the Goose Creek stratotype, belong to the lower unit. A reexamination of the Givhans Ferry collection (Appendices I and II, locality 23) housed in the U.S. National Museum and reported by Malde (1959) yielded 21 species of mollusks, 20 of which were held in common with other lower Goose Creek faunules.

Although a number of localities in our study are coincident with those studied by Cronin (1981; 1990) and Cronin *et al.* (1984), we have not studied the microfaunas and cannot apply fully the ostracode zonation. We suggest that the *Murrayina barclayi* zone is coincident with the lower Goose Creek Limestone, based on its occurrence at Givhan's Ferry State Park, and the *Paracytheridea mucra* zone is coincident with the upper Goose Creek Limestone, the Raysor Marl, and the Natural Well Duplin, based on occurrences at the Bear Bluff and Duplin stratotypes.

VI. MOLLUSCAN BIOSTRATIGRAPHY

Biostratigraphic Patterns

The biostratigraphic summaries are based on the distribution of 1127 species of Pliocene molluscs from approximately 180 localities in Virginia and the Carolinas. The analysis was made possible by stratigraphic revision in the study area (M. Campbell, 1992) and by the first documentation of statistically useful assemblages from the lower and upper units of the Goose Creek Limestone (Appendix II), from the Raysor Marl, and from the Elizabethtown, North Carolina, beds. Summary matrices for percentage and Dice statistics are provided (Table 2), which place the lower and upper Goose Creek Limestone units in biostratigraphic context with the remaining Pliocene units in the study area. The ranges of 27 index species are shown in Table 3.

Biostratigraphy or Biofacies ?

A legitimate argument against the stratigraphic model we are proposing is the premise that a number of the supposed biostratigraphic units are lateral biofacies rather than subdivisions of time (V.A. Zullo, 1991, personal communication). We are fully aware of the potential and complexities of environmental control of species distribution. The Beaufort Inlet estuary in North Carolina contains four distinct molluscan assemblages (Bird, 1970). The Recent molluscan assemblage patterns off the Carolinas from Cape Hatteras to Savannah include estuarine, littoral (inter-tidal), shallow sublittoral, inner shelf (Carolinian), mid-shelf (Caribbean), and outer shelf-upper slope assemblages (Porter and Safrit, 1981; Cerame-Vivas and Gray, 1966; USCS Recent collections). The percentage and Dice coefficient values (L. Campbell, unpublished data) between these Recent assemblages are similar in magnitude to the Pliocene values documented in Table 2. Sediment type and consolidation also influence molluscan assemblages. Species of *Nucula* and nuculanids thrive in fine-grained, silt-clay oozes, an environment hostile to most species (L. Campbell, 1993). The "live-bottom" hardgrounds off Charleston, South Carolina, provide a stable platform for hydroids, soft corals, sponges, and bryozoans, which then support an immense diversity of life, including mollusks.

Most Pliocene molluscan assemblages were, by comparison with the Recent patterns, aggregates of multiple biotopes mixed together with no discernable segregation. The lower and upper Waccamaw faunas both contain estuarine, intertidal, shallow sublittoral, inner, and mid-shelf genera and species, but the lower Waccamaw contains a greater percentage of mid-shelf taxa, the upper, a greater element of shallow sublittoral and inner shelf species. This difference results in greater diversity of lower Waccamaw faunules, and contributes to the greater extinction levels, because mid-shelf species generally

exhibit a greater endemism in time and space. Given assemblage patterns alone, one could argue for a shallowing-upward sequence deposited during the regressive phase of a single transgressive-regressive pulse, but the upper Waccamaw is unconformably separated from the lower unit, precluding that possibility.

The beds at Elizabethtown preserve littoral, shallow sublittoral, and estuarine species only (L. Campbell, 1993; Ward and Gilinsky, 1993), but the Duplin and Raysor returned to the diverse aggregate assemblage pattern. The Natural Well Duplin includes within a single layer, estuarine, intertidal, shallow sublittoral, inner, mid-, and outer shelf taxa. The shallow sublittoral and inner shelf species dominate in numbers of individuals, the mid-shelf species dominate in diversity of species present. *Cochliospira* (outer shelf) and *Donax* (intertidal) co-occur in the Timmonsville, South Carolina Duplin. As to aggregate assemblages, the Raysor Marl fauna differs from the Duplin Formation only in the absence of the estuarine and intertidal elements, *Donax* and ilyanassid species being conspicuously rare or absent.

In the study area, the Goose Creek Limestone calcarenites provide the only significant opportunity for lithofacies control over biofacies, and some taxa, such as *Placunanomia* and certain pectinids including *Nodipecten,* favored the calcarenites (Table 1). However, of the index species (Table 1) co-occuring in the upper Goose Creek Limestone calcarenites and Raysor Marl beds, only one also occurs (and that rarely) in the Duplin sands. The lower Goose Creek Limestone appears to consist mostly of inner-shelf species, but the upper Goose Creek fauna fully parallels the Raysor, with shallow, inner, mid-, and outer shelf elements jumbled in profusion.

Lyons (1989) has documented the nearshore molluscan assemblage of Hutchinson Island, Florida. This Recent fauna in many ways parallels the aggregate pattern of the Carolina Pliocene faunas. We suggest that milder Pliocene winters allowed a greater faunal mingling under conditions resembling the modern marine climates of the shallow shelf off central Florida. Secondly, we suggest that taxa, such as the volutid gastropods *Aurinia* and *Scaphella,* had a greater environmental tolerance during the Pliocene, based on their rare, but ubiquitous Pliocene distribution, and that their modern outer shelf-upper slope distribution is a refugium, atypical of their Neogene habitats. These premises satisfy part of the biofacies-averaging problem, but admixing and reworking of biotopes by bioturbation and physical processes was normative in the study area.

The aggregate nature of the Pliocene units argues for the greater importance of time as a causitive explanation for the statistical differences in Table 2. The Duplin estuarine fauna has no Raysor parallel, but that element was a small part of the total assemblage. Real differences existed between the Duplin and Raysor inner, mid-, and outer shelf assemblages. A comparison of Duplin and Elizabethtown estuarine, littoral, and shallow sublittoral species shows a higher similarity than a Duplin-Waccamaw comparison. Biofacies are important, and we believe that there is good evidence for a Raysor Marl-upper Goose Creek Limestone biofacies equivalency. Time, expressed by extinction, speciation, and colonization, remained the greater influence in determining the distinctive and evolving character of each successive assemblage.

Correlation with the Krantz Model and the Blackwelder M-Zones

Krantz (1991) has synthesized the global literature of oxygen isotope records to create a predictive model of Pliocene transgressions and regressions across the Atlantic Coastal Plain. Text-figure 1 illustrates the Krantz curve and our correlation of the Pliocene stratigraphic units in the study area.

The Raysor Marl and the lower and upper Goose Creek Limestone are constrained by the older, N-18, early Pliocene age of the subjacent K-1 Wabasso beds (zone 1, Yorktown equivalent) (Huddlestun, 1988) and the 3.2 Ma dating of the younger Duplin faunas. The lower Goose Creek contains a relatively high percentage of Miocene species (Table 2), and is framed by the Wabasso below and a significant unconformity above, conditions which best match the Krantz curve, K-3 transgression.

A distinct unconformity separates the Raysor Marl from the subjacent lower Goose Creek Limestone at the Martin Marietta Berkeley Quarry (M. Campbell, in preparation). The Raysor Marl and the upper Goose Creek Limestone appear to be biostratigraphically equivalent inshore siliciclastic and offshore leached calcarenite lithofacies, based on the common occurrence of a number of unusual index species (Table 1). However, the Krantz model provides three minor transgressions to which they might belong, the K-5, K-7, or K-9 incursions. Both the Raysor and upper Goose Creek contain common *Chesapecten septenarius,* a species that in Virginia disappeared before the K-9 level (L. Campbell, 1993). Finally, there is a relatively high commonality between the lower and upper Goose Creek Limestone faunas, although this could be the influence of common lithology rather than proximity of time. Of K-5 and K-7, K-5 is slightly greater in space and time (Text-figure 1). The Raysor Marl and upper Goose Creek Limestone are, therefore, assigned to K-5, but with a greater degree of uncertainty than exists for the other assignments.

Dowsett and Cronin (1990) documented an age of 3.5 to 3.0 Ma from deposits at Tar Heel, North Carolina (Robeson Farm), and the Lumber River. Although they assigned these beds to the Duplin Formation, both sites yield Raysor molluscan index species, including *Terebraspira elegans*, *Glycymeris americana* var. *abberans*, *Ecphora bradleyae*, and an undescribed *Scaphella* (Table 1). Natural Well-equivalent beds are also present at Tar Heel (Fig. 1, Bed E, of Britt *et al.*, 1992), but a bed-by-bed comparison of the Dowsett and Cronin (1990, Fig. 2, Locality 3) and the Britt versions of the Tar Heel section cannot be determined with certainty.

The Natural Well Duplin standard fauna includes 185 co-occurrences with the lower Waccamaw. In contrast, the Raysor standard fauna contains 94 co-occurences with the Waccamaw. The Duplin fauna is the most diverse Pliocene molluscan assemblage with 453 species, and contains a higher percentage of tropical species. Dowsett and Poore (1990) dated the Pliocene thermal maximum at 3.1 Ma. This maximum apparently coincides with the greatest westward incursion of the Pliocene sea. The Natural Well Duplin outcrop belt correspondingly occurs further westward, and at a higher elevation than the other Pliocene units in the study area. These lines of evidence are most consistent with the K-11 transgression. The Duplin, Raysor-upper Goose Creek, and lower Goose Creek molluscan assemblages are in the M-5 zone of Blackwelder (1981).

The beds at Elizabethtown, North Carolina (Carter *et al.*, 1988), best correlate with the Chowan River faunas in Virginia and the stratotype area (L. Campbell, 1993; Ward and Gilinsky, 1993). These contain a fauna older than the lower Waccamaw, younger than the Duplin (Table 2). Constrained by the respective ages of those two units, the Elizabethtown beds are assigned to K-13 to K-15. Zone M-4 of Blackwelder (1981) is the first-appearance-of-*Noetia limula* to last-appearance-of-*Glycymeris subovata* interval zone. *Glycymeris subovata (= G. hummi)* is common (Ward and Blackwelder, 1987) in an otherwise lower Waccamaw equivalent K-17 fauna at Aurora (L. Campbell, 1993), but makes its last appearance in the older Elizabethtown beds in southern North Carolina. Ward and Gilinsky (1993) document a high level of correlation between the faunules of the Elizabethtown beds and those of the stratotype Chowan River. We fully agree with that correlation, but dispute their assertion that the Elizabethtown is laterally equivalent with the Bear Bluff stratotype, a unit we document as being pre-, rather than post-, Natural Well Duplin.

The lower Waccamaw dates from 2.4 Ma based on the planktic foraminifera, and from 2.53 Ma by U-He coral dates from correlative deposits in southern Florida (Bender, 1973). These dates conform with the K-17 transgression. The lower Waccamaw fauna contains a greater diversity of midshelf species, the upper Waccamaw is dominated by littoral and shallow sublittoral species. This is consistent with the Krantz curve showing a greater incursion during the K-17 transgression.

The upper Waccamaw directly correlates with the upper Caloosahatchee of southern Florida, which unconformably underlies the 1.5 Ma Bermont beds. In turn, the upper Waccamaw is separated

from the lower Waccamaw by an unconformity at Calabash, North Carolina. As the lower Waccamaw at Calabash contains planktic foraminifera indicative of an age of 2.4 Ma (Huddlestun, 1975, personal communication), the upper Waccamaw is restricted to the interval, 1.5 to 2.4 Ma, which is conformable with K-19-21 on the Krantz curve (Fig. 1). The consequent age for the upper Waccamaw would be 1.9 to 2.2 Ma. This is older than the substantially younger published ages (Cronin *et al.*, 1984; Cronin, 1990; Bybell, 1990) of 1.8 to about 1.0 Ma.

Possible explanations for this disparity are: (1) that the upper Waccamaw (including Penholoway) mollusks survived the end-Caloosahatchee extinction event and are Bermont-equivalent; (2) that the planktic foraminifera and nannofossils used in the dating appeared earlier than is thought; or (3) that the deposits consist of admixed Bermont-equivalent and Waccamaw fossils. No Bermont-equivalent molluscan fauna has been documented in the Carolinas.

The Bermont fauna in Florida is essentially modern (85 percent extant), with some distinctive, tropical index species. The James City-upper Waccamaw-upper Cypresshead-lower Nashua-upper Caloosahatchee faunas form a zoogeographic continuum of warm temperate to subtropical to tropical molluscan species only approximately 50 percent extant. Pliocene extinction pressures were more severe to the north (L. Campbell, unpublished data), making a northern refugium highly unlikely. Planktic range zones may change, as shown by the Pliocene records of the supposedly Pleistocene *Globorotalia truncatulinoides* (Haq *et al.*, 1977). Such refinements are relatively minor, and we assume the planktic data to be essentially correct. Consequently, the simplist explanation may be that of mixed age micro- and macrofaunas. To further complicate the matter, Huddlestun (1988) reported an age of PL-5 for the Cypresshead Formation, based on planktic foraminifera, which is totally compatible with our macrofossil dating of the lower and upper Waccamaw.

The lower and upper Waccamaw faunas belong to the Blackwelder zone M-3. L. Campbell (1993) critiqued this zone, noting that the first appearance of the key indicator species, *Anadara ovalis*, fell within, rather than above, the upper Waccamaw.

Our stratigraphic model is based upon physical stratigraphy where superposition and unconformities can be demonstrated, and upon biostratigraphy, using index species and quantitative faunal statistics for correlation and for inferred position when physical evidence is lacking. This combination of "superposition and faunal statistics" (L. Campbell, 1993, p. 15) has been criticized by Ward and Gilinsky (1993, p. 8) as "at best, a comparison of apples and oranges." Superposition and biostratigraphy are both methods of determining relative time. They should be integrated where possible in any rigorous stratigraphic analysis. Problems arise when either physical stratigraphy or biostratigraphy is made subservient to the other. In our arguments concerning the validity of the Bear Bluff Formation, biostratigraphy can test the coherency of a proposed physical unit.

Ward and Gilinsky (1993, p. 8) also took the model (L. Campbell, 1993, fig. 1) to task for proposing impossible correlations, such as equating the Moore House member of the Yorktown Formation with the Chowan River beds. This is a mis-reading of the figure. A careful reading of the text (L. Campbell, 1993) will demonstrate that all columns were not intended to cross-correlate, but rather to reference individually the time line and Krantz isotope model, emphasizing contrast of age assignments rather than coincidence of units. This intent was not plainly re-stated in the figure caption by Campbell (1993, fig. 1), and any confusion created by that omission is regretted.

Similarly Text-figure 1 of the present work contrasts the prevailing stratigraphic model (Ward, Bailey, and Carter, 1991) with the one proposed by M. Campbell (1992). The prevailing model is a synthesis of the work of many noteworthy geologists, and has served coastal plain studies reasonably well for several decades. New evidence demonstrates that the prevailing model contained errors as to the age and relative position of the Goose Creek Limestone, and the nature of the Bear Bluff Formation. Further, the degree of complexity now demonstrable within the Pliocene strata of the study area poorly conforms with the prevailing model. The new

model recognizes the greater complexity and, coincidently, is compatible with most of the units predicted by the Krantz curve.

VII. SUMMARY

Recently discovered Goose Creek Limestone localities at the Martin Marietta Berkeley Quarry and around Conway, South Carolina, preserve both a rich and abundant calcitic fauna and a diverse moldic assemblage from which latex peels were taken. Small, seemingly disparate published faunules, including that of the stratotype at Goose Creek, are shown to be compatible subsets of these larger assemblages. Approximately 250 Goose Creek macrofossil species are now documentable in Charleston Museum, U.S. National Museum, or University of South Carolina Spartanburg collections, tripling the previous known diversity. Molluscan range zones support an early mid-Pliocene age for the Goose Creek Limestone, an age compatible with previous determinations from planktic foraminiferal zone PL-3 (Ward and Huddlestun, 1988, p. 73, section at Givhans Ferry State Park), and nannoplankton Zone NN 15 to mid-NN 14, or 3.9 to 3.2 Ma (Bybell, 1990).

The Goose Creek Limestone is divided by an unconformity into upper and lower units. These units are lithically identical, but may be distinguished biostratigraphically where faunules are sufficiently rich. All Conway area and Horry County mid-Pliocene calcarentites, including the stratotype of the "Bear Bluff Formation," belong to the upper Goose Creek Limestone. Upper Goose Creek localities in the Charleston area include Feteressa, the Seaboard Railroad ditch, and the Mark Clark Expressway pit. The Berkeley Quarry, the Givhans Ferry State Park section, and a number of Charleston localities, including the Goose Creek stratotype, belong to the lower unit.

Compounding errors in literature led to the placement of the Raysor Marl beneath the Goose Creek Limestone. The Goose Creek Limestone and the Tamiami Limestone contain common *Encope macrophora*. Cooke (1936) correctly correlated the two units, but he placed the Tamiami in the Waccamaw-equivalent Caloosahatchee Formation. Compounding the problem is a true Waccamaw-equivalent unit in the Charleston area, the "Smith's, Goose Creek" locality of Tuomey and Holmes (1855-1857). This upper bed at "Smith's" is best referred to the Cypresshead Formation of Huddlestun (1988). The actual order can be demonstrated in section at the Martin Marietta Berkeley Quarry, where the lower Goose Creek Limestone is unconformably overlain by the Raysor Marl.

In the Horry County area, the Bear Bluff Formation in literature contains parallel errors. DuBar (1987) described the Bear Bluff Formation as having a basal, leached calcarenite (bed A), a middle member (bed B) containing aragonite-preserved molluscan assemblages, and an upper, unfossiliferous sand (bed C). The basal calcarenite is equivalent to, and mappably contiguous with, the upper Goose Creek Limestone. Bed B strata at Calabash, North Carolina, and at various sites in Horry County, South Carolina, are lower Waccamaw, biostratigraphically equivalent to the shelly beds at "Smith's, Goose Creek." The Bear Bluff stratotype section contains only the basal, bed A calcarenites. Based on the stratotype section, the Bear Bluff Formation is synonymous with the Goose Creek Limestone, and localities assigned to the middle and upper members should be distributed among other formations.

So rectified, the lithostratigraphic and biostratigraphic units of the Carolinas become compatible with Pliocene sections proposed in Virginia and northern North Carolina (L. Campbell, 1993), Georgia (Huddlestun, 1988), and southern Florida (Scott and Allmon, 1992), and with the oxygen isotope-based sea-level curve of Krantz (1991).

VIII. SYSTEMATIC PALEONTOLOGY

Several important Goose Creek species that have been confused through rarity, misidentification, multiple names, or misleading illustrations are discussed here. Distribution is taken from sources and references cited in the systematic discussion and Appendices I and II.

Resolution of all systematic problems for the species listed in Appendix II is beyond the scope of this paper. Some taxa were simple to rectify, but other names, although dubious, could not be resolved

without reexamination of other relevant collections. Review of pertinent collections at Converse College (Howe, 1987), and the U.S. National Museum (Malde, 1959, and Cooke, 1936) resulted in nomenclatural changes and in a number of additional records.

GLYCYMERIS AMERICANA (Defrance)
Plate 5, figure 3

Pectunculus americanus DEFRANCE, 1826, Dict. Science Nat., v. 39, p. 225.
Pectunculus pulvinatus Lamarck. CONRAD, 1832, Foss. Shells Tert. Formations, p. 17, not of Lamarck, 1805.
Pectunculus lentiformis CONRAD, 1837, Foss. Shells Tert. Formations, p. 36.
Pectunculus carolinensis CONRAD, 1839, Foss. Medial Tertiary, inside back cover, later copies.
Pectunculus elephantopus H.C. LEA, 1846, Trans. Amer. Philos. Soc., ser. 2, v. 9, p. 230.
Pectunculus tricenarius CONRAD, 1845, Foss. Medial Tertiary, p. 63, pl. 35, fig. 1.
Pectunculus carolinensis HOLMES, 1859, Post-Pleiocene Foss. South Carolina, p. 15, pl. 3, fig. 4.
Axinaea lentiformis Conrad. MEEK, 1864, Smithsonian Misc. Coll., v. 7, p. 5.

VARIETIES OR SUBSPECIES:

Pectunculus passus CONRAD, 1845, Foss. Medial Tertiary, p. 64, pl. 35, fig. 3.
Pectunculus quinquerugatus CONRAD, 1845, Foss. Medial Tertiary, p. 63, pl. 34, fig. 3.
Pectunculus transversus TUOMEY and HOLMES, 1856, Pleiocene Foss. South Carolina, p. 51, pl. 17, fig. 6c; *non* Lamarck, 1819, Hist. Nat. Anim. Sans Vertèbres, v. 6, pt. 1, p. 55.
Glycymeris abberans NICOL, 1952, Jour. Wash. Acad. Sci., v. 42, p. 362; NICOL, 1953, Jour. Paleontology, v. 27, p. 451.

Description: In typical form, shell large, nearly circular, compressed; teeth large, taxodont with prominent hinge plate; beaks small, sharply pointed; ribs low, radial, smooth or consisting of crowded threads.

Occurrence: Glycymeris americana americana (Miocene ?) Pliocene to Recent. Virginia – Yorktown Zone 2, Chowan River; Carolinas – Yorktown Zone 2, Chowan River, lower and upper Goose Creek Limestone, Raysor, Duplin, Waccamaw; Florida – Pinecrest, Caloosahatchee; Recent – North Carolina to Florida. *Glycymeris americana* var. *quinquerugata* Pliocene. Virginia – Yorktown Zone 2; Carolinas – upper Goose Creek Limestone, Raysor, and Duplin; Florida – Pinecrest and Jackson Bluff. *Glycymeris americana* var.? *abberans* Pliocene. Carolinas – lower Goose Creek (type locality for *Pectunculus transversus* Tuomey and Holmes); upper Goose Creek Limestone and Raysor; Florida – lower or middle Pinecrest, especially around Miami.

Type localities: G. americana unknown; *G. a. abberans* Goose Creek, Charleston, South Carolina.

Discussion: Glycymeris americana (Defrance) is a large, circular, taxodont clam that is scarce in the Recent but quite common in the Pliocene of North and South Carolina. Some disparity exists in the publication date: Abbott (1974) cited 1829, whereas Sherborne (1923) cited 1826. In Duplin, Raysor, and Goose Creek populations, some specimens develop a set of strong ripples on the dorsal margins of the shell. Such shells were given the name *Glycymeris quinquerugata* (Conrad). Given this variation and intergradation, *G. quinquerugata* has been interpreted as a possible pathologic variety of *G. americana* (*e.g.*, Dall, 1898).

Tuomey and Holmes (1856) described *Pectunculus transversus* as a laterally elongate mold. Nicol (1952) noted that *Pectunculus transversus* is preoccupied and proposed the replacement name, *Glycymeris abberans*. Nicol's aragonitic specimens from Florida are laterally elongate and have a wrinkled, concentric shell ornamentation. Carter *et al.* (1988) figured a then-unique paired specimen of *Glycymeris* with sinuous concentric wrinkles completely crossing the disk. Carter (1988, personal communication) has suggested that *Glycymeris abberans* is an exceptionally rugate *Glycymeris americana* var. *quinquerugata*. The USC Spartanburg collection from the Mason Dixon pit at Conway contains over 100 internal and external molds of *Glycymeris abberans*. Most *G. americana* populations maintain a circular shell outline throughout ontogeny, but juvenile and subadult specimens of *G. abberans* display a remarkable allometric lateral expansion of the shell. The fully adult *Glycymeris abberans* specimens regain the circular shape, and the wrinkles either become obsolete or are expressed as large, concentric ripples. The Tuomey and Holmes, Nicol (1952), and University of North Carolina specimens show the elongate, subadult morphology. A small population of *Glycymeris americana* from the zone 2 Yorktown at Williamsburg, Vir-

ginia, has the laterally expanded subadult morphology, but lacks the wrinkling (USCS collections).

The rugate morphologies have different geologic ranges. *Pectunculus transversus (= Glycymeris americana* var. *abberans)* was originally described from the Goose Creek stratotype, a lower Goose Creek horizon. However, all subsequent records are from the upper Goose Creek Limestone and the Raysor Marl, suggesting that Tuomey and Holmes may have cited an erroneous locality. In the limestone, it co-occurs with normal and "quinquerugate" specimens. In the Raysor Marl, the three morphologies are joined by a fourth: a large, thick, and highly inflated shell, which may be the *Glycymeris americana* var. *passus* of Conrad. *Glycymeris americana* var. *quinquerugata* survived somewhat longer, co-occuring with typical, non-rugose stock in the Duplin of North and South Carolina. Only typical, non-rugate *Glycymeris americana* survived into the Waccamaw and the Recent. The diverse morphologies are considered herein provisionally to be varieties. More study will be necessary to resolve the questions of species, subspecies, genetic mutation and ecomorphism in this complex.

PECTEN HEMICYCLICUS Ravenel
Plate 1, figure 5; Plate 3, figure 6

Pecten hemicyclicus RAVENEL, 1834. Catalog of Recent Shells.

Janira hemicyclica (Ravenel). TUOMEY and HOLMES, 1855, Pleiocene Foss. South Carolina, p. 25.

Pecten ochlockoneensis MANSFIELD, 1932, Florida Geol. Survey, Bull. 8, p. 56, pl. 13, figs. 1, 3.

Pecten ochlockoneensis leensis MANSFIELD, 1939, Florida Geol. Survey, Bull. 18, p. 50, pl. 2, fig. 3.

Pecten raveneli Dall. CAMPBELL *et al.*, 1975, South Carolina Geol. Notes, v. 19, p. 82 (in part, mid-Pliocene records only).

Description: Shell large, subcircular, inequivalve, upper valve flat to weakly concave, lower valve convex, shallow in juvenile and typical adult specimens; ribs 20, low, with wider interspaces on upper valve. Very large specimens becoming laterally elongate, with the lower valve deeply cupped, the ventral margin of lower valve overlapping the upper valve.

Occurrence: Pliocene. Virginia – Yorktown, Zone 2; South Carolina – lower Goose Creek Limestone (common), upper Goose Creek Limestone (rare), Raysor (rare); Florida – Pinecrest and Jackson Bluff.

Type locality: The Grove Plantation, Charleston, South Carolina.

Discussion: *Pecten hemicyclicus* changed shape during ontogeny. Very large, laterally elongated shells, such as the type specimen, are not uncommon at Goose Creek localities but are rare in Florida. The smaller, more circular Florida

PLATE 1

Characteristic lower Goose Creek Limestone fossils from the Martin Marietta Berkeley Quarry, near Cross, South Carolina (locality 27). Illustrated specimens are deposited in the Charleston Museum.

Figures

1, 3. *Nodipecten collierensis* (Mansfield)
Size: # 1: 43 mm; Museum Catalog number ChM PI 9258
3: 43 mm; Museum Catalog number ChM PI 9259

2. *Chesapecten madisonius* (Say) subspecies ? *carolinensis* (Conrad)
Size: 84 mm; Museum Catalog number ChM PI 9260

4, 6. *Chesapecten septenarius* (Say)
Size: #4: 46 mm; Museum Catalog number ChM PI 9261
#6: 44 mm; Museum Catalog number ChM PI 9262

5. *Pecten hemicyclicus* Ravenel
Size: 49 mm; Museum Catalog number ChM PI 9263

7. *Amusium mortoni* (Ravenel)
Size: 52 mm wide; Museum Catalog number ChM PI 9264

8. *Spondylus* n. sp. ?
Size: 64 mm; Museum Catalog number ChM PI 9265

9. *Leptopecten leonensis* (Mansfield)
Size: 19 mm; Museum Catalog number ChM PI 9266

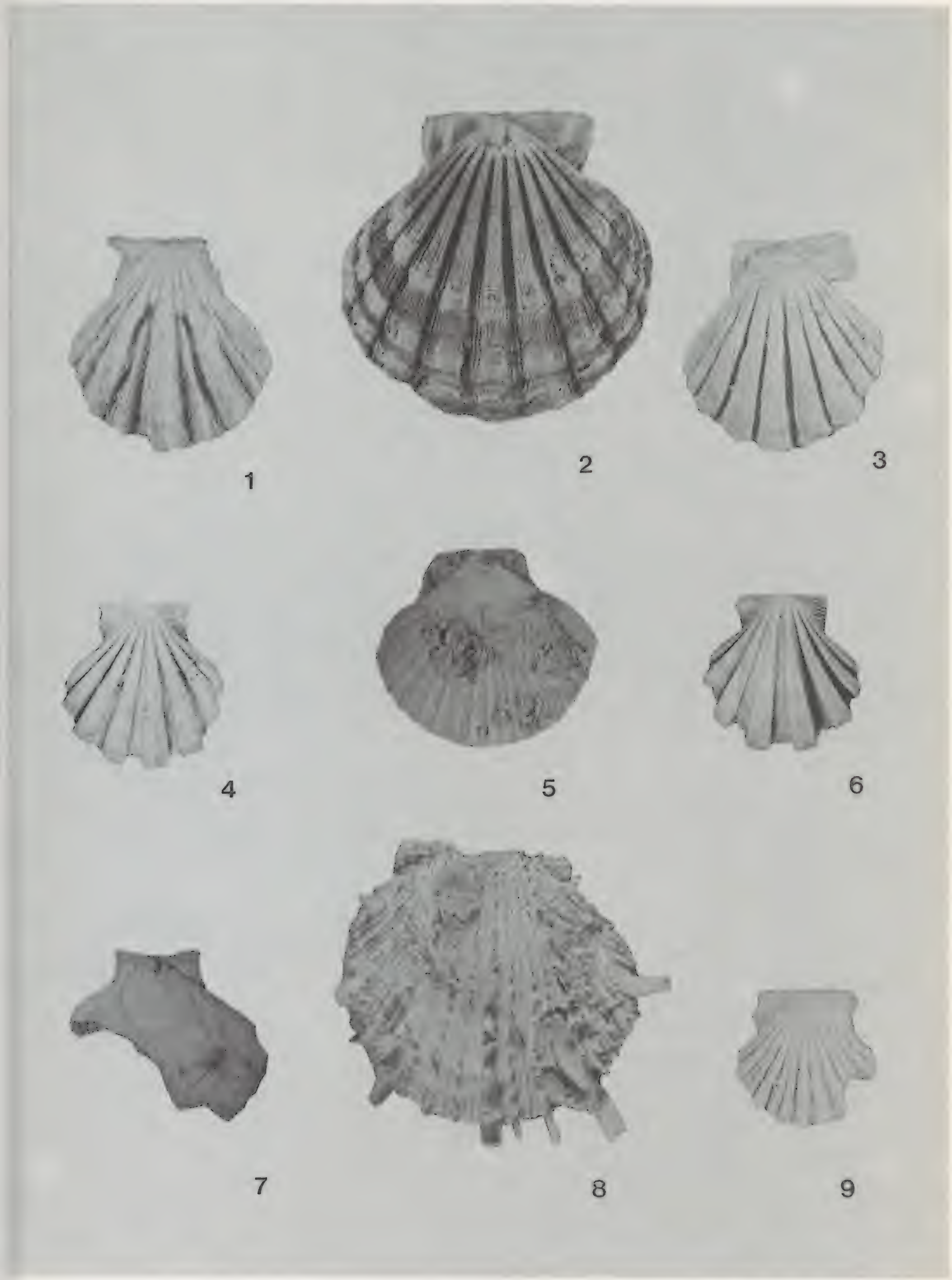


PLATE 1

specimens were named *Pecten ochlockoneensis* Mansfield, 1932, and *Pecten ochlockoneensis leensis* Mansfield, 1939. Reports of this species in the upper Pliocene Waccamaw Formation (Gibson, 1987, p. 41) or Recent (Dall, 1889, p. 32) appear to be incorrect, the Waccamaw report resulting from stratigraphic confusion, and the Recent report from misidentification.

Abbott (1974, p. 442) defined the subgenus *Euvola* as follows: "Lower or right valve very convex and with weak, rounded ribs; upper or left valve quite flat, more heavily sculptured. Type: *ziczac* (Linnaeus, 1758)." Fossil and Recent *Pecten (Euvola)* species are confused in both historic and current literature. In addition to *Pecten hemicyclicus* and its synonyms, there are *Pecten ziczac* (Linnaeus, 1758), *Pecten brouweri* Tucker, 1934 (see plate 5, figures 4 and 5), and two species covered under *Pecten raveneli* Dall, 1898.

Pecten ziczac, a Recent species, has 18 to 20 very low ribs with strong secondary ribbing in the interspaces. The right valve is convex but shallow. Its ribbing is distinct from that of the remaining taxa in which the interspaces lack the broad secondary ribbing. Its ribs are more elevated, and they are commonly grooved on the right valve. Recent shells called *Pecten raveneli* resemble *P. ziczac* and *P. hemicyclicus* in the shallow convexity of the right valve, but the Recent *P. raveneli* averages 25 ribs in contrast to about 20 ribs for *P. hemicyclicus*. The holotype of *P. raveneli* is a fossil from the "Caloosahatchee marls." Dall's figure (Dall, 1898, pl. 29, fig. 10) shows a substantially more convex shell, especially in the early growth. Fossil specimens of *P. raveneli* average 21 to 22 ribs. The Recent "*P. raveneli*" seems to be unnamed; it is being studied by Thomas Waller of the Smithsonian Institution.

Pecten brouweri differs from *P. raveneli* in having 14 to 16 ribs (Tucker, 1934). In outline, convexity of right valve, and absolute size attained, *P. brouweri* is very close to the holotype of *P raveneli*. *Pecten brouweri* is known from only a few specimens. All recovered in South Carolina are from the Goose Creek Limestone, considerably older than the "Waccamaw" age reported by Tucker (1934). Its rarity seems to be related to past unavailability of Goose Creek age deposits. The small population of *P. brouweri* in hand has a range of rib numbers from 14 to 20, placing it in close conformity with *P. raveneli*. *Pecten brouweri* is probably only subspecifically distinct from true *P. raveneli,* if not fully conspecific. Resolution of the problem will require larger populations than are now available.

Pecten ochlockoneensis violae Tucker, 1936, is here elevated to species status. *Pecten violae* is larger than *P. raveneli* and *P. brouweri*. The upper valve is concave for the first 10 mm of the disk, then becomes nearly flat. The upper valves of *P. raveneli* and *P. brouweri* are evenly concave across the entire disk. Typical specimens of *P. violae* have 15 to 16 radial ribs.

PLATE 2

Lower Goose Creek Limestone fossils from the Martin Marietta Berkeley Quarry (locality 27). Illustrated specimens are deposited in the Charleston Museum.

Figures

1. *Placunanomia burnsi* Mansfield
   Size: 67 mm; Museum Catalog number ChM PI 9267
2. *Placunanomia plicata* Tuomey and Holmes
   Size: 70 mm; Museum Catalog number ChM PI 9268
3. *Hyotissa haitensis* (Sowerby)
   Size: 73 mm; Museum Catalog number ChM PI 9269
4. *Encope macrophora* (Ravenel)
   Size: 37 mm; Museum Catalog number ChM PI 9270
5. *Busycon contrarium* (Conrad)
   Size: 50 mm; Museum Catalog number ChM PI 9271
6. *Ecphora quadricostata* (Say)
   Size: 86 mm; Museum Catalog number ChM PI 9272
7. *Turritella holmesi* Dall
   Size: 64 mm; Museum Catalog number ChM PI 9273

PLATE 2

LEPTOPECTEN LEONENSIS (Mansfield)
Plate 1, figure 9

Pecten leonensis MANSFIELD, 1932, Florida Geol. Survey, Bull. 8, p. 58, pl. 9, figs. 2, 3.
Pecten wendelli olgensis MANSFIELD, 1939, Florida Geol. Survey., Bull. 18, p. 51, pl. 2, figs. 1, 2, 4.

Description: Shell small, very thin, fragile; both valves convex, compressed; sculpture variable, typically, ribs 10-11, narrow, with wider interspaces, interspaces may have one to three radial threads. Auricles large.

Occurrence: Pliocene. Virginia – Yorktown, lower Zone 2; Carolinas – lower and upper Goose Creek Limestone, Raysor; Florida – lower Pinecrest and Jackson Bluff.

Type locality: Jackson Bluff, Leon County, Florida.

Discussion: Leptopecten wendelli (Tucker, 1934) has been synonymized with *Leptopecten leonensis* (Mansfield, 1932) by Ward and Blackwelder (1987, p. 140). However, Waccamaw specimens of *Leptopecten wendelli* from Calabash, North Carolina, are distinctive and are not conspecific with the older *Leptopecten leonensis*. *Leptopecten wendelli olgensis* is not morphologically similar to *L. wendelli*, but it seems to be conspecific with *L. leonensis*. Mansfield reported *L. leonensis* from the Ecphora zone of the Jackson Bluff Formation, from Porters Landing on the Savannah River, and a single specimen from Raysors Bridge. Tucker (1938) illustrated *L. leonensis* from supposed Waccamaw beds at Walkers Bluff on the Cape Fear River, which is also the type locality for *Pecten brouweri* Tucker, and *Carolinapecten eboreus* var. *walkerensis* Tucker, taxa that otherwise are restricted to faunules of the upper Goose Creek Limestone. It appears that Walkers Bluff contains reworked material or pre-Waccamaw strata, in addition to its better-known Waccamaw beds (Gardner, 1944). At the Berkeley Quarry, *L. leonensis* is fairly common in the lower Goose Creek Limestone, but is only rarely recovered from the younger Raysor sands.

Pecten harrisi Dall, 1898, may be another species of *Leptopecten* from the Caloosahatchee Formation.

CAROLINAPECTEN EBOREUS variety WALKERENSIS (Tucker)
Plate 3, figure 1; Plate 5, figures 1, 2

Pecten eboreus walkerensis TUCKER, 1934, Amer. Midland Nat., v. 15, p. 616, pl. 27, fig. 3.
Pecten eboreus buckinghamensis MANSFIELD, 1939, Florida Geol. Survey, Bull. 18, p. 53, pl. 3, figs. 4, 5, and 8.

PLATE 3

Pectenid bivalves from the upper Goose Creek Limestone at the Mark Clark Expressway pit (locality 13) and near Feteressa (locality 14). Illustrated specimens are deposited in the Charleston Museum.

Figures

1. *Carolinapecten eboreus walkerensis* (Tucker)
   Size: 92 mm; Museum Catalog number ChM PI 8365
   Locality: near Feteressa (loc. 14)
2. *Nodipecten peedeensis* (Tuomey and Holmes)
   Size: 111 mm; Museum Catalog number ChM PI 4164
   Locality: Mark Clark Expressway pit (loc. 13)
3. *Pecten* sp., possibly an immature *Pecten brouweri* Tucker
   Size: 18 mm; Museum Catalog number ChM PI 4178
   Locality: Mark Clark Expressway pit (loc. 13)
4. *Argopecten comparilis* (Tuomey and Holmes)
   Size: 63 mm; Museum Catalog number ChM PI 4166
   Locality: Mark Clark Expressway pit (loc. 13)
5. *Chesapecten septenarius* (Say), with attached *Ostrea sculpturata* Conrad
   Size: 114 mm; Museum Catalog number ChM PI 8351
   Locality: near Feteressa (loc. 14)
6. *Pecten hemicyclicus* Ravenel
   Size: 92 mm; Museum Catalog number ChM PI 4043
   Locality: Mark Clark Expressway pit (loc. 13)

1

2

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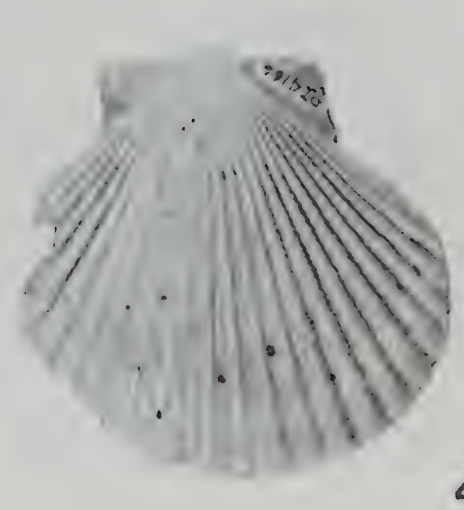

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PLATE 3

Description: Shell very large, subcircular, thin; right and left valves convex, compressed; ribs 20 to 24, low, narrow, with wide interspaces; posterior margin produced, left valve depressed, warped posteriorly.

Occurrence: Pliocene. Carolinas – upper Goose Creek Limestone, Raysor; Florida – Buckingham Limestone.

Type locality: Walker's Bluff, Cape Fear River, North Carolina.

Discussion: This is the largest of the *Carolinapecten* stock, with exceptional specimens exceeding 20 cm in maximum diameter. No other lineage or variety shows the pronounced expansion of the posterior margin or the warped cross section. Mansfield (1936, p. 174) erroneously synonymized *C. e. walkerensis* with Dall's (1900) *Pecten eboreus senescens.* The latter, which is the smallest of the forms of *Carolinapecten,* has subdued, nearly obsolete radial ribs, and a more inflated shell. This synonymy was accepted by Tucker-Rowland (1938, p. 50). Meanwhile, Mansfield (1939) described *Pecten eboreus buckinghamensis* from the Buckingham Limestone. The latter taxon was also described as large and having a warped cross-section, both traits uniquely shared with *C. e. walkerensis.* The warped cross-section becomes more obvious in specimens greater than approximately 10 cm in maximum diameter. *In situ,* abundant populations of *C. e. walkerensis* seem restricted to the Raysor Marl and the equivalent upper Goose Creek Limestone. Tucker (1934) designated a type locality of Walkers Bluff, Cape Fear River, North Carolina. However, she also cited a paratype from Nixon's, a classic Waccamaw locality, and USC Spartanburg collections contain single valves from basal Waccamaw beds at Calabash, North Carolina. In the Natural Well Duplin faunas, a smaller, more symmetrical *Carolinapecten eboreus* var. *darlingtonensis* (Dall) replaces the older *walkerensis* morphology. The reappearance of very rare, unpaired *walkerensis* valves in the Waccamaw consequently represents either retrograde evolution, an undetected surviving lineage, or reworking of older, Goose Creek specimens. At both Calabash and Nixon's, the Waccamaw rests unconformably on Cretaceous strata and contains reworked species. We consider the Waccamaw records of *C. e. walkerensis* to be fortuitous.

CHESAPECTEN MADISONIUS (Say)
variety (or ?subspecies) CAROLINENSIS
(Conrad)
Plate 1, figure 2

Pecten madisonius SAY, 1824, Jour. Acad. Nat. Sci. Phila., v. 4, p. 134.

Lyropecten carolinensis CONRAD, 1873, preprint of Appendix, Report of the Geological Survey of North Carolina, p. 18.

PLATE 4

Goose Creek Limestone fossils from the vicinity of Charleston, South Carolina. Illustrated specimens are deposited in the Charleston Museum, unless otherwise noted.

Figures

1. *Pecten anisopleura* Conrad
   Size: 84 mm; Museum Catalog number ANSP-unnumbered
   Locality: "40 miles south of Beaufort, N. Car." Dr. Yarrow
2. *"Spondylus holmesi"* Mazyck (manuscript name)
   Size: 110 mm; Museum Catalog number ChM PI unnumbered
   Locality: "from phosphate mines on the Cooper River, 10 miles from Charleston. Gift of Dr. Panknin."
3. *Encope macrophora* (Ravenel)
   Size: 43 mm; Museum Catalog number ChM PI 4485
   Locality: The Grove, Ravenel collection, part of the type lot.
4. *Mellita caroliniana* Ravenel
   Size: 62 mm; Museum Catalog number ChM PI 8374
   Locality: near Feteressa (loc. 14)

5, 6. *Malea* sp. cf. *M. densecostata* (Rutsch)
   Size: 79 mm; Museum Catalog number ChM PI 8372
   Locality: near Feteressa (loc. 14)

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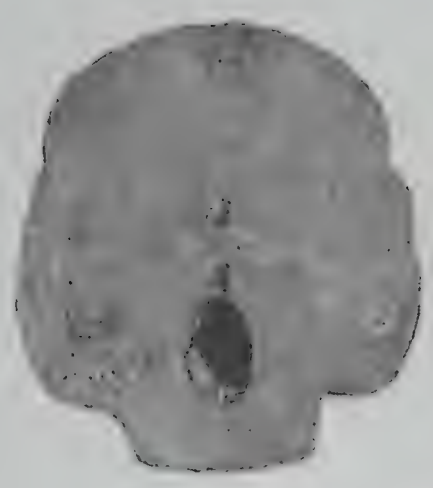

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PLATE 4

Chesapecten madisonius (Say). WARD and BLACKWELDER, 1975, U. S. Geol. Survey, Prof. Paper 861, p. 16, pl. 6, figs. 1-4; pl. 7, figs. 1, 7, 8; GIBSON, 1987, Smithsonian Contrib. Paleobiology, no. 61, p. 73, pl. 22, fig. 1; pl. 24, figs. 3-5; pl. 25, figs. 1-4, 6; pl. 26, figs. 1, 3-5.

Description: Shell large, subcircular, heavy; right and left valves convex; ribs 10 to 14, narrow, with strong, scaled cords.

Occurrence: Pliocene. Virginia – Yorktown, basal Zone 2; Carolinas – Yorktown, basal Zone 2 (Aurora), lower Goose Creek Limestone; Florida – Tamiami Limestone.

Type locality: North Carolina.

Discussion: Chesapecten madisonius is rare in the Goose Creek Limestone. The scant material present varies from 10 to 14 ribs. Gibson (1987) reported *C. madisonius* with similar low rib counts from the Lee Creek mine, Aurora, North Carolina. Typical specimens of *C. madisonius* from higher in the section have 16 to 22 ribs. This low rib-number morphology has been called *Lyropecten carolinensis* Conrad, 1873 (holotype in the Academy of Natural Sciences Philadelphia). *Lyropecten carolinensis* would become *Chesapecten madisonius carolinensis* (Conrad) if it proves to be a valid subspecies. It does not co-occur with typical *C. madisonius*. Too few specimens are presently available to resolve the question. *Chesapecten septenarius* and *Chesapecten jeffersonius* produced rare individuals with 10 to 12 ribs, but *C. madisonius* may be recognized by its narrower ribs and coarse radial threads with strong scaling.

Chesapecten septenarius (Say)
Plate 1, figures 4, 6; Plate 3, figure 5

Pecten septenarius SAY, 1824, Jour. Acad. Nat. Sci. Phila., v. 4, p. 136, pl. 9, fig. 3.

Chesapecten septenarius (Say). WARD and BLACKWELDER, 1975, U.S. Geol. Survey, Prof. Paper 861, p. 15, pl. 6, figs. 5-7, pl. 7, figs. 2, 9.

Chesapecten jeffersonius septenarius (Say). GIBSON, 1987, Smithsonian Contrib. Paleobiology, no. 61, p. 71, pl. 21, figs. 7-8; pl. 22, figs. 2-3; pl. 23, figs. 1-3; pl. 24, figs. 1-2; pl. 25, fig. 5; pl. 26, fig. 2.

Description: Shell large, subcircular, very heavy; right and left valves convex, well inflated; ribs 4 to 12, wide, squared or laterally expanded at the crest; ribs with secondary sculpture of fine striations, scaling weak at edge of ribs, or lacking.

Occurrence: Pliocene. Virginia – Yorktown, lower and middle Zone 2; Carolinas – Yorktown, lower Zone 2, lower and upper Goose Creek Limestone, Raysor; Florida – Tamiami Limestone and lower Jackson Bluff.

Type locality: "Maryland" [unknown Virginia locality].

Discussion: Chesapecten septenarius is a highly variable species, similar in some of its morphologies to the older to contemporaneous *Chesapecten jeffersonius*. *Chesapecten septenarius* has between four and twelve ribs that vary in cross-section

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PLATE 5

Mollusks from the Mason Dixon pit, upper Goose Creek Limestone, Conway, South Carolina (locality 69). Illustrated specimens are deposited in the Charleston Museum.

Figures

1, 2. *Carolinapecten eboreus walkerensis* (Tucker); showing the concave outline of the right flank
Size: 110 mm; Museum Catalog number ChM PI 12420

3. *Glycymeris americana abberans* Nicol, and *Pleioptygma carolinensis* (Conrad); latex peels
Size: 59 mm; Museum Catalog number ChM PI 12421

4. *Pecten brouweri* Tucker; flat upper valve
Size: 35 mm; Museum Catalog number ChM PI 12422

5. *Pecten brouweri* Tucker; deeply cupped lower valve
Size: 44 mm; Museum Catalog number ChM PI 12423

6. *Argopecten anteamplicostatus* (Mansfield)
Size: 28 mm; Museum Catalog number ChM PI 12424

7. *Ecphora bradleyae* Petuch
Size: 34 mm; Museum Catalog number ChM PI 12425

8. *Terebrispira elegans* (Emmons); latex peel
Size: 78 mm; Museum Catalog number ChM PI 12426

PLATE 5

between "T" topped, square, and slightly rounded morphologies. *Chesapecten jeffersonius* typically has seven to nine lower, rounded ribs. The latter is more characteristic of deposits below the Goose Creek Limestone, such as the Zone 1 Yorktown Formation to the north, or the Wabasso beds. However, Stanley (1988, personnal communication) has paired specimens of *C. jeffersonius* from the Tamiami Formation (bed 11, APAC pit, Sarasota, Florida), a formation that is faunally equivalent to the lower Goose Creek Limestone. Sloan specimens from "Raysor's Bridge" figured by Ward and Huddlestun (1988) seem to conform with *C. jeffersonius* morphologies. We have found no such specimens in either the Goose Creek or Raysor levels at the Berkeley Quarry. Pooser (1965, p. 23) and Colquhoun (1965, p. 46) reported *Chesapecten jeffersonius* from a pond near Orangeburg, but subsequent collections from the site contain only *Chesapecten septenarius*.

NODIPECTEN PEEDEENSIS
(Tuomey and Holmes)
Plate 3, figure 2

Pecten peedeensis TUOMEY, 1848, Rept. Geol. South Carolina, p. 176 (nude name); TUOMEY and HOLMES, 1855, Pleiocene Foss. South Carolina, p. 30, pl. 12, figs. 1-5.

Pecten vaccamavensis OLSSON, 1914, Bulls. Amer. Paleontology, v. 5, no. 24, p. 11, pl. 1, fig. 1.

Nodipecten peedeensis (Tuomey and Holmes). M. CAMPBELL, 1988, South Carolina Acad. Sci. Bull., v. 50, p. 35; M. CAMPBELL, 1988, Amer. Malacol. Union, Program and Abstracts, p. 39; SMITH, 1991, U.S. Geol. Survey, Prof. Paper 1391, p. 94, pl. 15, figs. 1-4.

Not *Pecten peedeensis* Tuomey and Holmes. MANSFIELD, 1936, Jour. Paleontology, v. 10, no. 3, p. 180; TUCKER-ROWLAND, 1938, Mém. Mus. Royal Hist. Nat. Belgique, Ser. 2, fasc. 13, p. 23.

Description: Shell large, subcircular, well inflated; ribs high, nodes large; upper valve with seven large, prominently noded ribs, alternating in strength, lower valve with eight subequal ribs, nodes rare or absent. Secondary sculpture of coarse radial threads crossed by finer concentric lines. Concentric resting stages often stepped or shelved.

Occurrence: Pliocene. Carolinas – upper Goose Creek Limestone.

Type locality: Near Giles Bluff, Pee Dee River, South Carolina.

Discussion: Nodipecten peedeensis was originally cited (Tuomey, 1848) as occurring with two lower to mid-Pliocene taxa, *Chesapecten septenarius* and *Ecphora quadricostata* (Campbell *et al.*, 1975, p. 82, 110; Blackwelder, 1981, p. 3). The type specimens of *N. peedeensis* were temporarily misplaced in the American Museum of Natural History. In their absence, Tucker-Rowland (1938, p. 23) designated a misidentified European specimen as neotype (Smith, 1988, personal communication).

Two morphologies exist within the Goose Creek Limestone material now at hand: a smoother, less sculpted shell typified by the Berkeley quarry population (over 200 specimens); and shells from the Mason Dixon pit, Conway, South Carolina, with higher ribs, somewhat stronger secondary sculpture, and higher and more frequent nodes. In addition to the stronger sculpture, the Mason Dixon specimens are very large, sometimes exceeding 160 mm in maximum diameter. The Mason Dixon population also includes abnormal morphologies, which we intrepret as genetic mutants. The weaker ribs of the mutant left valve are reduced or eliminated, producing five instead of seven ribs, and the right valve correspondingly has the four central ribs fused into two wide ribs. A small population from the Charleston area has similar normal and mutant morphologies. M. Campbell (1988a, 1988b) first interpreted the Charleston and Berkeley quarry populations as variation within a single species. With the 1989-1990 discovery of a large population (over 120 specimens) of *N. peedeensis* from the Mason Dixon pit, we now conclude that two species-level taxa are involved. The Berkeley Quarry specimens best conform with *N. collierensis* (Mansfield), but the Mason Dixon and Charleston specimens better conform with the holotype of *N. peedensis*. A detailed morphological study is in progress.

NODIPECTEN COLLIERENSIS (Mansfield)
Plate 1, figures 1, 3

Pecten (Nodipecten) pitteri collierensis MANSFIELD, 1932, U.S. Geol. Survey, Prof. Paper 170-D, p. 47, pl. 16, figs. 3, 5.

Nodipecten peedeensis (Tuomey and Holmes). M. CAMPBELL, 1988, South Carolina Acad.

Sci. Bull., v. 50, p. 35; M. CAMPBELL, 1988, Amer. Malacol. Union, Program and Abstracts, p. 39.

Nodipecten collierensis (Mansfield). SMITH, 1991, U.S. Geol. Survey, Prof. Paper 1391, p. 90, pl. 8, figs. 5-6, pl. 9, figs. 3-4, pl. 10, figs. 1-6, pl. 11, fig. 1.

Description: Shell medium to large, subcircular, slightly compressed; ribs low, nodes typically low, occasionally absent; upper valve with seven low, narrow ribs alternating in strength; lower valve with eight subequal ribs. Secondary sculpture of fine radial threads.

Occurrence: Pliocene. Carolinas – lower Goose Creek Limestone; Florida – Tamiami Limestone, lower Pinecrest.

Type locality: About 11 miles northeast of Marco, Collier County, Florida.

Discussion: Nodipecten collierensis differs from *N. peedeensis* in its smaller size, lower inflation, and less vigorous sculpture. Shelving at resting stages is weak or absent. The large population from the Berkeley Quarry is remarkably uniform in morphology, varying principally in degree of node development.

Spondylus species
Plate 1, figure 8

Spondylus sp. TUOMEY and HOLMES, 1855, Pleiocene Foss. South Carolina, p. 24.

Spondylus bostrychites Sowerby. OLSSON and PETIT, 1964, Bulls. Amer. Paleontology, v. 47, no. 217, p. 515, not of Sowerby, 1850.

Description: Shell large, oval, well inflated, reaching 175 mm; larger shells becoming thick and massive. Spines irregular, low and irregular in some specimens; when well developed, with rows of well developed large, flat spines alternating with zones of much smaller, needle-like spines.

Occurrence: Pliocene. South Carolina – lower and upper Goose Creek Limestone, Raysor (on contact with lithified lower Goose Creek Limestone): Florida – Tamiami Limestone and Pinecrest beds.

Type locality: Undescribed.

Discussion: Conrad (1873) described "*Pecten anisopleura*" from "40 miles south of Beaufort, N. C." (which is off the present coast). This unique specimen is figured here for the first time (plate 4, figure 1). It is a fossil *Spondylus*, quite different from the *Spondylus* in the Goose Creek Limestone. Rather, *Spondylus anisopleura* seems conspecific with the Eocene species, *Spondylus lamellacea*, later described by Kellum (1926). "40 miles south of Beaufort, N. C." might refer to the Wilmington, North Carolina, area where *Spondylus lamellacea* is common in the Castle Hayne Limestone. Regrettably, the unique holotype of *Pecten anisopleura* was lost while being returned to the Academy of Natural Sciences by registered mail. Because of the doubt concerning the affinities of *S. anisopleura*, its decrepit condition, and its postal demise, we suggest that the species concept be restricted to the holotype (plate 4, figure 1).

Tuomey (1848) and Tuomey and Holmes (1855) documented but did not figure a species of *Spondylus* from fragments in limestone at Goose Creek. In the Charleston Museum, there is a very spiny specimen (plate 4, figure 2) of a Goose Creek species, with a note saying that Mazyck intended to describe the species as "*Spondylus holmesi.*" However, that name was not cited in the catalog of Mazyck's published species (Clench, 1967, p. 43). Stanley (personal communication, 1990) has suggested that the Mazyck specimen probably is referable to *Spondylus rotundatus* Dall. It becomes the first record of that species from the Goose Creek Limestone and the first record of the species north of Florida.

More recently, excavations at the APAC pit, Sarasota, Florida, have uncovered a number of specimens of an undescribed species that have been referred to *Spondylus bostrychites* Sowerby, 1850 (Olsson and Petit, 1964, p. 515), a species apparently restricted to the Caribbean. The new Florida species matches the common Goose Creek morphology from South Carolina. Several large fragments and rare complete single valves of this new species have been found at the Berkeley Quarry near Cross, at the G.& C. pit west of Conway, and near Charleston, South Carolina. As Stanley is describing the species from better Floridian material, the Goose Creek material will remain unnamed for the present.

Placunanomia plicata Tuomey and Holmes
Plate 2, figure 2

Placunanomia plicata TUOMEY and HOLMES, 1855, Pleiocene Foss. South Carolina, p. 19, pl. 6, figs. 4-6.

Description: Shell of moderate size, thin, smooth, calcitic, trigonal; margin highly plicate;

hinge structure of large cardinal crurae in right valve, corresponding socket in left valve.

Occurrence: Pliocene. Virginia – Yorktown, middle Zone 2; Carolinas – lower and upper Goose Creek Limestone, Raysor, Duplin; Florida – Tamiami Limestone, Pinecrest, Jackson Bluff.

Type locality: Smith's, Goose Creek, Charleston, South Carolina, basal beds.

Discussion: Placunanomia plicata is variable in the number and extent of the plications. Typical *Placunanomia plicata* with thin shells and well developed marginal folds are found in both the lower and upper zones of the Goose Creek Limestone, and in the Raysor Marl. In younger Duplin beds rare specimens are thicker-shelled and have smaller and more numerous marginal undulations. Insufficient material is available for determining systematic status of the latter morphology.

PLACUNANOMIA BURNSI (Mansfield)
Plate 2, figure 1

Pododesmus burnsi MANSFIELD, 1939, Florida Geol. Survey, Bull. 18, p. 55, pl. 4, figs. 1, 3, 5, 6.

Placunanomia pinella GARDNER, 1945, Nautilus, v. 59, p. 39, pl. 4, figs. 1, 2, 5, 6.

Placunanomia (Tamianomia) burnsi (Mansfield). OLSSON, 1967, Some Tertiary Mollusks from South Florida and the Caribbean, p. 9, pl. 1, figs. 4-4b.

Description: Shell of moderate size, irregularly oval; margin even or fluted; sculpture of radial threads; hinge structure of large cardinal crurae in right valve, corresponding socket in left valve.

Occurrence: Pliocene. South Carolina, lower Goose Creek Limestone; Florida – Tamiami Limestone.

Type locality: Station 3300, Shell Creek, Florida.

Discussion: The radial threads are diagnostic. *Placunanomia burnsi* is an index species for the Tamiami Formation in southern Florida (Olsson, 1967). This is the first record of the species north of Florida.

HYOTISSA HAITENSIS (Sowerby)
Plate 2, figure 3

Ostrea haitensis SOWERBY, G. B., I., 1850, Quart. Jour. Geol. Soc. London, v. 6, p. 53.

Ostrea meridionalis HEILPRIN, 1886, Trans. Wagner Free Inst. Sci., p. 100, pl. 14, figs. 35, 35a.

Ostrea tamiamiensis MANSFIELD, 1932, U.S. Geol. Survey, Prof. Paper 170-D, p. 46, pl. 14, figs. 1, 3.

Ostrea tamiamiensis monroensis MANSFIELD, 1932, U.S. Geol. Survey, Prof. Paper 170-D, p. 46, pl. 15, figs. 1-4.

Hyotissa haitensis (Sowerby). WILSON, 1987, Smithsonian Contrib. Paleobiology, no. 61, p. 16.

Description: Shell large, broadly trigonal, variably plicate; shell structure microscopically vesicular; hinge flanked by vermiform corrugations. Spines prominant, weakly developed, or absent.

Occurrence: Miocene. Florida – Chipola. Pliocene. Carolinas – lower and upper Goose Creek Limestone, Cape Fear River, North Carolina, Conway, and the Berkeley Quarry; Florida – Tamiami Limestone, Pinecrest.

Type locality: "Haiti" [unknown Dominican Republic locality].

Discussion: South Carolina specimens of *Hyotissa haitensis* are predominantly the spineless morphology.

MALEA species cf. MALEA DENSECOSTATA (Rutsch)
Plate 4, figures 5, 6

Dolium galea Linnaeus. TUOMEY and HOLMES, 1856, Pleiocene Foss. South Carolina, p. 139, in part, not pl. 28, fig. 11.

Tonna (Malea) ringens densecostata RUTSCH, 1934, Abhl. Schweiz. Paleontol. Gesell., v. 54, p. 60, pl. 111, figs. 6, 7.

Malea densecostata (Rutsch). OLSSON and PETIT, 1964, Bulls. Amer. Paleontology, v. 47, no. 217, p. 554, pl. 79, figs. 5, 5a.

Malea sp. unnamed moldic species. PETUCH, 1989, Nautilus, v. 103, p. 92.

Description: Shell large, well inflated; spire high, whorls convex; sculpture of numerous strong spiral ribs, number uncertain on the mold. Aperture distorted, typical of the genus.

Occurrence: Pliocene. Carolinas – upper Goose Creek Limestone; Florida – Tamiami Limestone, lower Pinecrest.

Type locality: Punta Gavilan, Venezuela.

Discussion: The Charleston Museum collections contain a mold of *Malea* species, probably *Malea densecostata,* from Fetteressa, a Charleston locality near the Seaboard Coast line (Weems *et al.*, 1982, p. H142). The USC Spartanburg collections contain a small population of internal molds from the Mason Dixon pit. This species probably is the *"Dolium galea"* of Tuomey and Holmes, 1856, but their illustration is not that of a tun shell. Campbell and Campbell (1977, p. 113) suggested that Tuomey and Holmes' figure represents an

internal mold of a *Busycon*. With the large collection of Goose Creek molds now in hand, the Tuomey and Holmes figure best matches a broken specimen of *Ficus*.

Petuch (1989) stated that the Tamiami moldic *Malea* is a new species distinct from *M. densecostata*, but neither described nor figured the form. The South Carolina specimens are compatible with the *M. densecostata* morphologies to the extent determinable by internal molds. Discovery of an external mold will be necessary to completely resolve the question.

ECPHORA QUADRICOSTATA (Say)
Plate 2, figure 6

Fusus 4-costata SAY, 1824, Jour. Acad. Nat. Sci. Phila., v. 4, p. 127, pl. 7, fig. 5.
Colus quadricostatus (Say). TUOMEY and HOLMES, 1857, Pleiocene Foss. South Carolina, p. 149.
Fusus umbilicatus "Wagner." DALL, 1898, Trans. Wagner Free Inst. Sci., v. 5, p. 9, pl. 2, fig. 2.
Ecphora parvicostatus PILSBRY, 1911, Proc. Acad. Nat. Sci. Phila., v. 63, p. 438, fig. 1.
Ecphora striatula PETUCH, 1986, Jour. Coastal Research, v. 2, p. 406, pl. 3, figs. 15, 16.
Ecphora quadricostata (Say). WILSON, 1987, Smithsonian Contrib. Paleobiology no. 61, p. 21; WARD and GILINSKY, 1988, Notulae Naturae, no. 469, p. 11, pl. 5, figs. 1-4 (extensive discussion and synonymy).
Ecphora hertweckorum PETUCH, 1987, Nautilus, v. 101, p. 204, figs. 14, 15.
Ecphora violetae PETUCH, 1988, Bull. Paleomalacology. v. 1, p. 35, pl. 1, figs. 1-3, 6.
Ecphora floridana PETUCH, 1988, Field Guide to the Ecphoras, p. 67, fig. 30.
Ecphora quadricostata rachelae PETUCH, 1988, Field Guide to the Ecphoras, p. 69, fig. 33.
Ecphora mansfieldi PETUCH, 1988, Field Guide to the Ecphoras, p. 129, pl. A1, figs. A, E.
Ecphora quadricostata leecreekensis PETUCH, 1988, Field Guide to the Ecphoras, p. 131, pl. A2, fig. E.
Ecphora pachycostata PETUCH, 1988, Field Guide to the Ecphoras, p. 130, pl. A1, fig. D.

Description: Shell large, calcitic, well inflated; umbilicus flaring; aperture large, circular; ribs four, spiral, rib-crests narrow or slightly expanded; secondary sculpture of spiral threads weak or absent.

Occurrence: Pliocene. Virginia – Yorktown, zones 1 and 2; Carolinas – Yorktown, zones 1 and 2, lower and upper Goose Creek Limestone, Raysor, Duplin (rare); Florida – Tamiami Limestone, lower Pinecrest, Jackson Bluff (*Ecphora* zone).

Type locality: "Maryland" [unknown Virginia locality].

Discussion: Ecphora quadricostata recently has been given several names (Petuch, 1988), that seem to be, at best, varieties. Although found in beds of lower and mid-Pliocene age from Virginia to Florida, *E. quadricostata* is common from South Carolina to Florida only in the lower Goose Creek Limestone, the Raysor Marl and the *Ecphora* zone of northwestern and southern Florida.

ECPHORA BRADLEYAE Petuch
Plate 5, figure 7

Ecphora bradleyae PETUCH, 1987, Nautilus, v. 101, p. 204, figs. 1-6.

Description: Shell large, calcitic, well inflated; umbilicus flaring; aperture large, circular; ribs four, spiral, rib-crests wide, strap-like, touching or nearly touching adjacent crest; interspaces narrow, uniform in sub-adult specimens, central interspace becoming proportionally wider in large adults.

Occurrence: Pliocene. Carolinas – upper Goose Creek Limestone, Raysor; Florida – lower and middle Pinecrest.

Type locality: APAC pit, Sarasota, Florida.

Discussion: Ecphora bradleyae is the only species of *Ecphora* found in the upper Goose Creek Limestone at the Mason Dixon pit, but it co-occurs with *Ecphora quadricostata* as a rare element in Raysor assemblages at the Martin Marietta Berkeley Quarry, at Lynchburg, South Carolina, and at Tar Heel, North Carolina (Carter *et al.*, 1988). *Ecphora bradleyae* seems to be a short-lived species useful for correlation.

ENCOPE MACROPHORA (Ravenel)
Plate 2, figure 4; Plate 4, figure 3

Scutella macrophora RAVENEL, 1844, Proc. Acad. Nat. Sci. Phila., v. 2, p. 334.
Encope macrophora (Ravenel). TUOMEY and HOLMES, 1855, Pleiocene Foss. South Carolina, p. 3, pl. 1, fig. 3.
Macrophora macrophora CONRAD, 1865, Proc. Acad. Nat. Sci. Phila. v. 17, p. 74.
Macrophora raveneli CONRAD, 1865, Proc. Acad. Nat. Sci. Phila. v. 17, p. 74.
Encope macrophora tamiamiensis MANSFIELD, 1932, U.S. Geol. Survey, Prof. Paper 170-D, p. 48, pl. 17, fig. 8.
Encope tamiamiensis Mansfield. COOKE, 1959, U.S. Geol. Survey, Prof. Paper 321, p. 48, pl. 17, figs. 3, 4; KIER, 1963, Smithsonian Misc.

Coll., v. 145, no. 5, p. 36, pl. 14, figs. 1-6.

Description: Disk small to rather large (Goose Creek specimens average 30-35 mm), oval, truncate posteriorly; outline typical of the genus (arrowhead sand dollars). Lunule circular to oval. Margin rounded, may become thickened in large specimens. Relative proportions highly variable.

Occurrence: Pliocene. Virginia – Yorktown, middle Zone 2; South Carolina – lower Goose Creek Limestone (common), upper Goose Creek Limestone (rare), Raysor (rare); Florida – Tamiami Limestone, lower Jackson Bluff.

Type locality: The Grove Plantation, Charleston, South Carolina.

Discussion: Encope macrophora is common to abundant in the Tamiami Limestone of southern Florida, where it has been called *Encope tamiamiensis* Mansfield, 1931 (D. Campbell, 1987). Cooke (1936) considered *Encope macrophora tamiamiensis* to be an index fossil for the Tamiami Limestone, which he incorrectly interpreted as a member of the Caloosahatchee Formation. Consequently, *E. macrophora* was an important part of the evidence for assigning a Caloosahatchee and, therefore, Waccamaw-equivalent age to the Goose Creek Limestone. Both Cooke (1959) and Kier (1963) believed Mansfield's taxon to be distinct, but cited different criteria. The much larger population of *Encope macrophora* from the Berkeley Quarry shows a range of variation fully compatible with *E. tamiamiensis* (D. Campbell, 1987).

IX. LITERATURE CITED

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X. APPENDIX I: LOCATION, STATISTICAL AND INDEX SPECIES BIOSTRATIGRAPHY, AND STRATIGRAPHIC ASSIGNMENT OF GOOSE CREEK LIMESTONE LOCALITIES

BIOSTRATIGRAPHIC UNITS
R = ALSO RECENT; UW = UPPER WACCAMAW; LW = LOWER WACCAMAW; D = NATURAL WELL DUPLIN; RA = RAYSOR; UGC = UPPER GOOSE CREEK; LGC = LOWER GOOSE CREEK; M = ALSO MIOCENE; N = NUMBER OF TAXA IN FAUNULE; K- = TRANSGRESSIVE ONLAP UNIT FROM FIGURE 1.

LOCALITIES

1. NEAR GILES'S BLUFF (Tuomey, 1848)

"Giles's Bluff (on the Pee Dee River, Marion County) on the land of Henry Davis, Esq." and "some distance from the river" (Tuomey, 1848, p. 175). Recent efforts to locate Giles's Bluff have been unsuccessful, but Tuomey (1848, p. 136) sketches Cretaceous section along the Pee Dee River, which if drawn to scale places the site about halfway between Britton's Ferry and Birch's Ferry.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 18	38.9	50.0	38.9	72.2	72.2	88.9	72.2	11.1
DICE TOTAL		.050	.051	.033	.055	.115	.163	.190	.032

INDEX SPECIES: *Nodipecten peedeensis, Chesapecten septenarius, Ecphora quadricostata*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone (K-5).

2. GOOSE CREEK (Tuomey, 1848) (Stratotype locality)

"Bluff along Goose Creek, 0.3 km east of the Seaboard Coastline railroad bridge over Goose Creek in the North Charleston 7 1/2 min. quadrangle." (Weems *et al.*, 1982, p. H137.)

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 14	14.3	50.0	50.0	85.7	71.4	100	72.2	11.1
DICE TOTAL		.014	.040	.033	.051	.090	.146	.180	.049

INDEX SPECIES: *Encope macrophora, Pecten hemicyclicus*
STRATIGRAPHIC ASSIGNMENT: lower Goose Creek, based on common *Encope*, (K-3).

3. GOOSE CREEK (Tuomey and Holmes, 1855-1857)
(same as locality 2)

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 12	33.3	50.0	41.7	83.3	58.3	83.3	83.3	33.3
DICE TOTAL		.029	.034	.024	.043	.063	.105	.153	.067

INDEX SPECIES: *Encope macrophora, Glycymeris abberans**
STRATIGRAPHIC ASSIGNMENT: lower Goose Creek Limestone (K-3).

*Type locality for *Pectunculus transversus* Tuomey and Holmes, which was renamed *Glycymeris abberans* Nicol, 1953.

4. GOOSE CREEK (Weems *et al.*, 1982)
(same as locality 2)

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 4	00.0	75.0	75.0	75.0	75.0	100	100	25.0
DICE TOTAL		.000	.018	.015	.013	.028	.044	.065	.018

INDEX SPECIES: *Pecten hemicyclicus*
STRATIGRAPHIC ASSIGNMENT: lower Goose Creek Limestone, (K-3).

Encope macrophora and *Pecten hemicyclicus* are common only in the lower Goose Creek Limestone, rare and very local in the upper unit.

5. THE GROVE (Tuomey, 1848)
"Cooper River.– .. The Grove, residence of Dr. Edmund Ravenel." (Tuomey and Holmes, 1855, p. xi). Berkeley County "east of Cooper River and 5 miles northwest of Wando" (C. W. Cooke, 1936, p. 129).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 6	16.7	67.8	67.8	83.3	83.3	100	83.3	50.0
DICE TOTAL		.007	.023	.019	.026	.047	.065	.080	.053

INDEX SPECIES: *Encope macrophora, Pecten hemicyclicus*
STRATIGRAPHIC ASSIGNMENT: lower Goose Creek, based on common *Encope* (K-3).

6. THE GROVE (Tuomey and Holmes, 1855-1857)
(see locality # 5)

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 6	16.7	67.8	67.8	83.3	83.3	100	83.3	50.0
DICE TOTAL		.007	.023	.019	.022	.047	.065	.080	.035

STRATIGRAPHIC ASSIGNMENT: Goose Creek Limestone (K-3 to 5).

7. SMITH'S GOOSE CREEK (Tuomey and Holmes, 1855-1857). Aragonite shell.
"Goose Creek.-- The plantation of the late Geo. Henry Smith, Esq." (Tuomey and Holmes, 1855, p. xi). Note: this site has been equated by Cooke (1936) with Yeaman Hall (see locality #24).

		R	UW	LW	D	RA	LGC	UGC	M
% TOTAL	N = 25	52.0	72.0	76.0	44.0	24.0	36.0	24.0	12.0
DICE TOTAL		.090	.100	.088	.046	.051	.089	.083	.045

INDEX SPECIES: *Pecten holmesi*
STRATIGRAPHIC ASSIGNMENT: lower Cypresshead Formation (lower Waccamaw equivalent) (K-17).

8. RAYSOR BRIDGE (Ward & Huddlestun, 1988)

Exact location uncertain, as Sloan gave disparate directions, see Huddlestun (1988) for details. According to Pooser (1965, p. 72), north bank of Edisto River, 7.8 miles S. 4 degrees W. from St. George, or 4.1 miles S. 84 degrees W. from Grover.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 47	17.0	42.5	46.8	70.2	80.8	70.2	51.1	55.3
DICE TOTAL		.051	.104	.097	.132	.297	.293	.298	.335

INDEX SPECIES: *Leptopecten leonensis, Chesapecten jeffersonius, Chesapecten madisonius carolinensis,* elongate *Astarte*

STRATIGRAPHIC ASSIGNMENT: mixed Raysor (K-5) and lower Goose Creek Limestone (K-3), Raysor (aragonite preserved element) predominates.

9. CROSS (Ward & Huddlestun, 1988)

Berkeley County near Cross, SC, on the east side of County Road 59, about two miles south of State Highway Rt. 6, Chicora 7.5 minute quadrangle. From Santee, South Carolina, follow Rt. 6 east to Eutawville,and Eutaw Springs. Approximately 3 3/4 miles east of Eutaw Springs, turn south on State Route S-59. The Berkeley Quarry is approximately 2 miles south on the east side of the highway. It is obvious from the road. The quarry contains Eocene Santee Limestone, which is mined for road metal, overlain by Pliocene Raysor sands and lower Goose Creek Limestone. Active quarrying regularly expose and destroy new fossiliferous sections. Permission must be obtained at the office.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 28	21.4	53.6	57.1	75.0	89.3	78.6	60.7	50.0
DICE TOTAL		.041	.082	.074	.087	.211	.214	.231	.206

INDEX SPECIES: *Chesapecten septenarius*

STRATIGRAPHIC ASSIGNMENT: Raysor (K-5).

10. ORANGEBURG dug pond, Pooser, 1965; Colquhoun, 1965; L. Campbell, manuscript

Orangeburg County, east of the city of Orangeburg, 400 yards from Rt. S-38-65, 4.4 miles east of the intersection of S.C. 33 and S-38-65. (Colquhoun, 1965, stop Nine, p. 45).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 2	00.0	00.0	00.0	50.0	100	100	100	00.0
DICE TOTAL		.000	.000	.000	.004	.019	.022	.033	.000

INDEX SPECIES: *Chesapecten septenarius*

STRATIGRAPHIC ASSIGNMENT: Raysor (K-5)

11. TEARCOAT BRANCH (Ward and Huddlestun, 1988)

0.6 miles southwest of intersection of Highway 255 with County Rt. 58, 3.9 miles south of intersection of Rt. 58 and Rt. 378, about 4 miles east of the intersection of Rt. 378 and the Sumter bypass. Site effectively obliterated by Hurricane Hugo.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 24	20.8	50.0	58.3	100	95.8	75.0	62.5	66.7
DICE TOTAL		.035	.067	.065	.101	.197	.178	.210	.242

STRATIGRAPHIC ASSIGNMENT: Duplin (K-11).

Note the high Raysor correlation, which is a function of the small and selective data set.

12. TEARCOAT BRANCH S. Campbell, 1974; and manuscript in progress.
(see locality # 11)

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 336	21.4	38.4	39.9	100	47.6	38.4	25.6	19.6
DICE TOTAL		.240	.384	.361	.847	.587	.502	.378	.297

INDEX SPECIES: *Melanella magnoliana, Coralliophila leonensis, Phos sloani*
STRATIGRAPHIC ASSIGNMENT: Duplin (K-11).

13. MARK CLARK EXPRESSWAY (Charleston Museum collections)
Charleston County, South Carolina; borrow pit for Mark Clark Expressway, east of SC Rt. 61 between Bull Creek and Ashley Hall Plantation Road; 32 degrees 48.8 minutes North, 80 degrees 1.6 minutes West, John's Island 7.5' quadrangle.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 14	7.1	35.7	57.1	50.0	57.1	100	71.4	14.3
DICE TOTAL		.007	.029	.038	.030	.072	146	.150	.033

INDEX SPECIES: *Pecten brouweri, Pecten hemicyclicus, Chesapecten septenarius, Nodipecten peedeensis*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone

14. NEAR FETTERESSA (Charleston Museum collections)
Seaboard Railroad Ditch, Charleston County, South Carolina; north ditch along Seaboard Coast Line Railroad south of Dorsey Ave., about 1.45 km west of Dorchester Road overpass (SC Rt. 642); 32 degrees 51.2 minutes North, 80 degrees 2.5 minutes West, John's Island 7.5' quadrangle.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 10	10.0	50.0	60.0	70.0	80.0	100	70.0	20.0
DICE TOTAL		.007	.029	.029	.030	.073	.106	.109	.034

INDEX SPECIES: *Encope macrophora, Chesapecten septenarius, Nodipecten peedeensis, Malea densecostata*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone

15. LOMAX-KING PIT (Florida State Museum, new this study)
Lomax-King pit, Charlotte County, Florida, Punta Gorda 7.5 minute quadrangle, southeast quarter.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 9	00.0	22.2	33.3	44.4	55.6	88.9	77.8	33.3
DICE TOTAL		.000	.012	.014	.017	.046	.086	.109	.051

INDEX SPECIES: *Encope macrophora, Leptopecten leonensis, Chesapecten septenarius*
STRATIGRAPHIC ASSIGNMENT: Tamiami Limestone

16. CROSS Howe, 1987, and Converse College Collections
(see locality # 9)

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 48	18.7	41.7	41.7	81.2	91.6	70.8	66.7	37.5
DICE TOTAL		.058	.104	.088	.156	.342	.301	.383	.231

INDEX SPECIES: *Encope macrophora, Pecten hemicyclicus, Chesapecten septenarius*
STRATIGRAPHIC ASSIGNMENT: mixed Raysor and lower Goose Creek

17. PINECREST BEDS, SARASOTA Petuch, 1982; Hunter, 1971
Macasphalt Co. Newburn Pit Mine, northeast of Sarasota, Florida. Bed 11.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 23	8.7	21.7	26.1	43.5	60.9	52.2	65.2	21.7
DICE TOTAL		.014	.028	.028	.042	.121	.119	.211	.076

INDEX SPECIES: *Encope macrophora, Chesapecten septenarius*
STRATIGRAPHIC ASSIGNMENT: Tamiami Limestone

18. GOOSE CREEK C. W. Cooke, 1936
"Bluff on S. E. bank of Goose Creek, 1/3 mile east of S. A. L. and 3/4 mile S. E. of Melgrove, Berkeley Co. S. Car." (Cooke locality label).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 6	00.0	50.0	50.0	83.3	66.7	100	66.7	16.7
DICE TOTAL		.000	.018	.015	.022	.037	.065	.064	.018

INDEX SPECIES: *Encope macrophora, Pecten hemicyclicus*
STRATIGRAPHIC ASSIGNMENT: Goose Creek Limestone, data insufficient for more precise assignment.

19. PEEDEE RIVER Tuomey and Holmes, 1855-1857; specific sites unknown.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 50	26.0	46.0	40.0	90.0	58.0	78.0	44.0	26.0
DICE TOTAL		.083	.119	.088	.179	.224	.342	.260	.165

STRATIGRAPHIC ASSIGNMENT: equivocal, percentage favors Duplin, DICE favors Raysor, but the commonality with the Goose Creek Limestone and the Miocene rather strongly favor Raysor.

20. CROSS Campbell *et al.*, 1975
(see locality # 9)

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 15	26.7	20.0	20.0	53.3	73.3	33.3	40.0	13.3
DICE TOTAL		.029	.017	.014	.034	.098	.052	.090	.033

INDEX SPECIES: *Pecten hemicyclicus*
STRATIGRAPHIC ASSIGNMENT: Raysor (K-5).

21. GODFREY FERRY BRIDGE, PEE DEE RIVER, Malde, 1959
"South side of Pee Dee River at excavation for new bridge abutment on U. S. Highway 378, 7-8 feet above river level" (Malde, 1959, p. 32).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 23	21.7	52.2	47.8	82.6	69.6	95.6	82.6	30.4
DICE TOTAL		.035	.067	.051	.080	.138	.219	.268	.107

INDEX SPECIES: *Pecten hemicyclicus*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone.

22. DAVIS LANDING, PEE DEE RIVER, Malde, 1959
"Davis Landing, highest rock exposed, 12-15 feet above base of Duplin" (Malde locality label).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 16	12.5	43.7	43.7	75.0	81.2	87.5	75.0	18.7
DICE TOTAL		.014	.040	.033	.051	.116	.144	.178	.048

INDEX SPECIES: *Ecphora bradleyae*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone.

23. GIVHANS FERRY, EDISTO RIVER, Malde, 1959

"Givhans Ferry State Park, East bank, Edisto River, 20 feet above stream, ca 500 feet upstream from park bldg. C. Wythe Cooke locality 170" (Malde locality label).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 21	19.0	52.4	57.1	95.2	76.2	85.7	95.2	28.6
DICE TOTAL		.028	.062	.056	.089	.139	.181	.286	.093

INDEX SPECIES *Pecten hemicyclicus*

STRATIGRAPHIC ASSIGNMENT: lower Goose Creek Limestone.

24. 0.4 MILES SOUTH OF YEAMANS HALL, Malde, 1959

"Pridgen borrow pit 2000 ft. south of Yeaman Hall gate (Melgrove quad.) from spoil dredged from bottom of pit, midpoint south side of ponded water" (Malde locality label).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 34	11.8	47.0	44.1	85.3	55.9	82.4	82.4	23.5
DICE TOTAL		.027	.086	.068	.119	.156	.264	.366	.113

INDEX SPECIES: *Pecten hemicyclicus, Carolinapecten eboreus walkerensis*

STRATIGRAPHIC ASSIGNMENT: somewhat equivocal, assigned to upper Goose Creek Limestone based on *C. e. walkerensis.*

25. McDOWELL TUNNEL Malde, 1959

"Inlet shaft on Foster Creek" (Malde, 1959, p. 32).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 3	00.0	66.7	66.7	100	100	100	33.3	00.0
DICE TOTAL		.000	.012	.010	.013	.028	.033	.016	.000

STRATIGRAPHIC ASSIGNMENT: probably upper Goose Creek Limestone, but data insufficient for any certain assignment.

26. McDOWELL TUNNEL (Shaft 1), Malde, 1959

Further detail not specified.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 25	12.0	48.0	48.0	80.0	84.0	80.0	92.0	28.0
DICE TOTAL		.021	.066	.056	.084	.179	.197	.319	.105

INDEX SPECIES: *Pecten hemicyclicus*

STRATIGRAPHIC ASSIGNMENT: lower Goose Creek Limestone (K-3).

27. CROSS, *Encope* level, new, USCS collections

(see locality # 9)

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 100	23.0	35.0	39.0	75.0	69.0	82.0	92.0	30.0
DICE TOTAL		.126	.161	.154	.271	.447	.590	.840	.288

INDEX SPECIES: *Encope macrophora, Pecten hemicyclicus, Leptopecten leonensis, Chesapecten madisonius carolinensis, Chesapecten septenarius, Nodipecten collierensis*

STRATIGRAPHIC ASSIGNMENT: lower Goose Creek Limestone (K-3).

28. CROSS, *Mercenaria* level, new, USCS collections
(see locality # 9)

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 197	22.8	40.6	45.2	89.3	94.9	53.8	39.1	27.4
DICE TOTAL		.195	.300	.295	.542	.921	.565	.487	.354

INDEX SPECIES: *Glycymeris abberans, Chesapecten septenarius, Ecphora bradleyae, Terebraspira elegans, Mercenaria tridacnoides*
STRATIGRAPHIC ASSIGNMENT: Raysor (K-5).

29. SARASOTA, *Mercenaria* level, Petuch, 1982; Hunter, 1971
(see locality # 17), Bed 10.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 39	30.7	33.3	48.7	71.8	69.2	74.3	64.1	23.1
DICE TOTAL		.079	.069	.085	.114	.218	.267	.316	.122

INDEX SPECIES: *Anadara propatula*
STRATIGRAPHIC ASSIGNMENT: lower Pinecrest beds (K-5).

30. SMITH'S, GOOSE CREEK, Tuomey and Holmes, 1855-1857, mold and calcitic shell, basal bed.
(see locality #7).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 2	00.0	00.0	00.0	00.0	00.0	100	50.0	00.0
DICE TOTAL		.000	.000	.000	.000	.000	.022	.017	.000

INDEX SPECIES: *Malea densecostata*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone (K-5), based on index species.

31. LAKE WACCAMAW, NC, Olsson, 1914; Richards, 1950; DuBar, 1971
Columbus County, NC, north shore of Lake Waccamaw, from the Pumping Station eastward (Richards, 1950, p. 29).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 5	20.0	80.0	80.0	80.0	80.0	100	60.0	40.0
DICE TOTAL		.007	.023	.019	.017	.037	.055	.048	.035

INDEX SPECIES: *Nodipecten peedeensis*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone (K-5), based on index species. Note: DuBar *et al.* (1974) placed this in their Bear Bluff Formation.

69. MASON DIXON PIT, CONWAY, SC, new, USCS collections (M. Campbell). Calcite and mold preservation only.
From Conway, South Carolina, follow Rt. 701 south. From the point at which 701 changes from four to two lanes, travel approximately 2 miles south. Site is visible on east side of the highway, but was inactive in 1991.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 152	20.4	36.8	41.4	78.3	62.5	94.0	48.7	26.3
DICE TOTAL		.149	.230	.225	.393	.526	.867	.546	.308

INDEX SPECIES: *Glycymeris abberans, Pecten brouweri, Chesapecten madisonius carolinensis, Carolinapecten eboreus walkerensis, Nodipecten peedeensis, Ecphora bradleyae*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone (K-5).

103. G & C MINING CO., new, USCS collections (M. Campbell).
From Conway, South Carolina, follow Rt. 378 west approximately 5 miles to Cedar Grove Church. High spoil piles are visible from the highway. Turn north by company sign. Permission must be obtained at the office.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 13	00.0	23.1	23.1	69.2	76.9	92.3	53.8	38.5
DICE TOTAL		.000	.017	.014	.039	.090	.126	.106	.083

INDEX SPECIES: *Pecten brouweri, Carolinapecten eboreus walkerensis, Nodipecten peedeensis*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone (K-5).

104. THOMPKINS MINING CO. new, USCS collections (M. Campbell).
From Conway, South Carolina, take Rt. 905 north approximately 3 miles from the city limits. Turn left at company sign. 18 meters of leached upper Goose Creek Limestone calcarenite are preserved, unconformably overlying the Cretaceous Pee Dee Limestone. Permission must be obtained at the office.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 35	14.3	37.1	45.7	77.1	80.0	91.4	57.1	28.6
DICE TOTAL		.033	.070	.072	.111	.230	.300	.260	.140

INDEX SPECIES: *Pecten brouweri, Carolinapecten eboreus walkerensis*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone (K-5).

105. BEAR BLUFF STRATOTYPE new, USCS collections (M. Campbell).
This site can be successfully examined only by boat. From Conway, South Carolina, take Rt. 905 north to Hickory Grove. Turn east on State Rt. 105. Travel approximately 4 miles to the Waccamaw River. Park at the public boat landing beside the bridge. Launch boat and travel approximately 1 mile north. The stratotype is on the east bank just before a large bend in the river.

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 27	31.0	62.1	62.1	93.1	89.7	100	69.0	51.7
DICE TOTAL		.061	.099	.083	.112	.218	.280	.270	.219

INDEX SPECIES: *Carolinapecten eboreus walkerensis*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone (K-5).

134. WALKER'S BLUFF CALCARENITE Walker's Bluff, Cape Fear River, North Carolina (from literature).

		R	UW	LW	D	RA	UGC	LGC	M
% TOTAL	N = 5	40.0	40.0	40.0	20.0	20.0	60.0	20.0	20.0
DICE TOTAL		.015	.012	.010	.004	.009	.033	.016	.018

INDEX SPECIES: *Leptopecten leonensis, Carolinapecten eboreus walkerensis, Pecten brouweri*
STRATIGRAPHIC ASSIGNMENT: upper Goose Creek Limestone (K-5).

XI. APPENDIX II: CHECK LIST OF GOOSE CREEK MACROFOSSILS

Locality data is coded by number: detailed locality data and statistical analyses are shown in Appendix I. Systematics follow L. Campbell (1993).

BIVALVIA

Nucula proxima Say, 1822; latex cast
27, 69, 104, 105

Nuculana acuta (Conrad, 1832); latex cast
27, 69

Barbatia leonensis Mansfield, 1932; latex cast, internal mold
69

Striarca centenaria Say, 1824; latex cast
69

Anadara (Granoarca) propatula (Conrad, 1844); internal mold
26

Anadara lienosa (Say, 1832); internal and external molds, latex cast
26, 27, 69, 104

Anadara improcera (Conrad, 1845); internal and external molds, latex cast
23, 69, 105

Anadara improcera buccula (Conrad, 1845); latex cast
69

Noetia trigintinaria (Conrad, 1862); internal mold
27, 69

Noetia incile (Say, 1824); internal mold
22, 27

Quadrilateria adamsi (Dall, 1886); latex cast
69

Glycymeris americana abberans Nicol, 1952; internal and external molds, latex cast
3, 69

Glycymeris americana americana (Defrance, 1826); internal and external molds
27, 69, 104, 105

Glycymeris americana quinquerugata (Conrad, 1841); internal and external molds
26, 27, 69

Glycymeris duplinensis Dall, 1898; latex cast
69

Glycymeris subovata (Say, 1824); internal mold
27, 69, 103, 104, 105

Modiolus gigas (Dall, 1898); internal and external molds
1, 19, 24, 27, 69

Lithophaga sp.; external mold and burrow linings
27

Atrina harrisi Dall, 1898; internal and external mold
69, 104

Pteria colymbus (Röding, 1798); calcitic shell
27, 69

Pecten brouweri Tucker, 1934; calcitic shell
13, 69, 103, 104

Pecten sp. cf. *Pecten biformis* Conrad, 1843; calcitic shell
27 (reworked Oligocene species)

Pecten hemicyclicus Ravenel, 1834; calcitic shell
2, 4, 6, 13, 18, 20, 21, 24, 26, 27

Leptopecten leonensis (Mansfield, 1932); calcitic shell
27, 134

Amusium mortoni (Ravenel, 1844); calcitic shell
1, 2, 4, 5, 6, 13, 14, 18, 20, 22, 24, 25, 26, 27, 69, 104

Carolinapecten eboreus eboreus (Conrad, 1833); calcitic shell
5, 6, 21, 22, 23, 24, 25, 26, 27

Carolinapecten eboreus walkerensis (Tucker, 1934); calcitic shell
24, 69, 103, 104, 105

Argopecten comparilis (Tuomey and Holmes, 1855); calcitic shell
13, 24, 27, 69

Argopecten anteamplicostatus (Mansfield, 1936); calcitic shell
69, 104

Chesapecten jeffersonius (Say, 1824); calcitic shell
8, bed of Savannah River

Chesapecten madisonius (Say, 1824) spp.; calcitic shell
27, 69

Chesapecten septenarius (Say, 1824); calcitic shell
1, 13, 14, 27, 103

Nodipecten collierensis (Mansfield, 1931); calcitic shell
27

Nodipecten peedeensis (Tuomey and Holmes, 1855); calcitic shell
1, 13, 14, 31, 69, 103

Chlamys decemnarius (Conrad, 1834); calcitic shell
27

Plicatula marginata Say, 1824; calcitic shell
13, 18, 21, 24, 26, 27, 69, 104

Spondylus sp.; calcitic shell
2, 3, 13, 27, 103

Spondylus rotundatus Heilprin, 1886; calcitic shell
Charleston, Mazyck collection

Anomia simplex Orbigny, 1842; calcitic shell
27, 69

Placunanomia burnsi (Mansfield, 1939); calcitic shell
27

Placunanomia plicata Tuomey and Holmes, 1856; calcitic shell
13, 27, 30, 69

Limaria pellucida (C.B. Adams, 1846); calcitic shell
24, 69

Limaria carolinensis (Dall, 1898); calcitic shell
24, 27, 69
Ostrea compressirostra Say, 1824; calcitic shell
2, 4, 5, 6, 13, 14, 21, 22, 23, 24, 26, 27, 31, 69, 103, 104, 105
Ostrea sculpturata Conrad, 1840; calcitic shell
4, 13, 14, 18, 21, 22, 24, 26, 27, 69, 103, 104, 105
Ostrea locklini Gardner, 1945; calcitic shell
27, mouth of Four Hole Swamp from Sloan collections
Hyotissa haitensis (Sowerby, 1850); calcitic shell
27, 69
Cubitostrea sellaeformis (Conrad, 1832); calcitic shell
104 (reworked, Eocene species)
Exogyra costata Say, 1820; calcitic shell
69 (reworked, Cretaceous species)
Linga pensylvanica (Linnaeus, 1758); internal mold
24, 27
Lucinisca cribraria (Say, 1824); latex cast
27
Radiolucina tuomeyi (Dall, 1903); external mold, latex cast
23, 27, 69, 105
Parvilucina crenulata (Conrad, 1840); latex cast
105
Parvilucina multilineata (Tuomey and Holmes, 1856); latex cast
23, 69
Callucina keenae Chavan, 1971; latex cast
69
Ctena speciosa (Rogers and Rogers, 1837); latex cast
23, 27, 69, 103, 105
Pseudomiltha anodonta (Say, 1824); internal mold
2, 24, 27, 69
Divalinga quadrisulcata (Orbigny, 1842); latex cast
26, 27, 69, 105
Diplodonta acclinis (Conrad, 1832); latex cast
24, 69
Diplodonta punctulata (H.C. Lea, 1843); latex cast
24, 27, 69, 104, 105
Diplodonta subvexa (Conrad, 1834); latex cast
69, 103, 104
Chama congregata (Conrad, 1833); latex cast
1, 22, 69
Chama emmonsi Nicol, 1953; latex cast
69
Pseudochama corticosa (Conrad, 1833); latex cast
27, 69
Arcinella cornuta (Conrad, 1866); latex cast
1, 20, 27, 69
Aligena striata H.C. Lea, 1843; latex cast
69, 105
Cyclocardia granulata (Say, 1824); latex cast
21, 26, 27, 69, 105
Pleuromeris sp.; latex cast
69
Pteromeris abbreviata (Conrad, 1841); latex cast
69
Astarte floridana Dall, 1903; internal mold
69
Astarte vaughani Mansfield, 1916; latex cast
26, 27, 69
Astarte concentrica Conrad, 1834; latex cast
26, 27, 69, 103
Astarte undulata Say, 1824; latex cast
24, 26, 69
Eucrassatella speciosa (Adams, 1852); latex cast
23, 24, 26, 27, 69
Eucrassatella Virginica (Gmelin, 1791); internal and external molds
23, 27, 69
Crassinella lunulata (Conrad, 1834); internal mold
69
Planicardium virginianum (Conrad, 1839); internal mold
69
Planicardium acutilaqueatum (Conrad, 1839); internal mold
21, 22, 24, 26, 27, 69, 103, 104
Dinocardium robustum (Lightfoot, 1786); internal mold
1, 26, 27, 69, 104
Laevicardium sublineatum (Conrad, 1841); internal mold
1, 24, 26
Papyridae sp. aff. *P. soleniformis* (Bruguière, 1789); internal and external mold
21, 24, 69
Spisula similis (Say, 1822); internal mold
27
Raeta alta Conrad, 1873; internal mold
1
Mulina congesta (Conrad, 1833); internal and external mold
27, 69, 105
Ensis directus (Conrad, 1844); internal mold, latex cast
5, 6, 23, 26, 27, 69, 105
Tellina aequistriata Say, 1824; latex cast
69
Hemimetis magnoliana (Dall, 1900); internal and external molds, latex cast
2, 27, 69, 104
Macoma virginiana (Conrad, 1866); internal mold
23
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LIFE HISTORY AND DEVELOPMENT OF OLIGOCENE LARGER BENTHIC FORAMINIFERA: A TEST OF THE ENVIRONMENTAL CONTROL ON HETEROCHRONY

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I. ABSTRACT

Larger benthic foraminifera (LBF) comprise a heterogeneous group of protists that typically reach more than three cubic millimeters in test volume and have complex internal morphologies. For most extant species, large size and complex tests are related to algal symbiosis. Living forms are associated with coral reefs and related oligotrophic carbonate environments, where symbiotic relationships with algae are especially advantageous. Extinct larger foraminifera are almost invariably associated with similar (paleo)environments. It has been argued on theoretical grounds (and supported by some empirical data) that in stable (*i.e.*, low energy) but stressful (*e.g.*, low light for photosymbionts) conditions, the semelparous LBF will delay reproduction, grow to larger sizes, and produce larger embryons (juvenile tests) during asexual reproduction. To test these relations, test size and embryon size of the LBF *Nummulites panamensis*, *Lepidocyclina mantelli*, *L. yurnagunensis*, and *L. undosa*, were examined along a Lower Oligocene forereef-to-deep shelf transect across Georgia, Florida, and Alabama.

The results of this study indicate that intraspecific LBF body size and embryon size are predicted to be greatest at the extremes of a species' range. At these limits, however, it is suggested that large size is attained for different reasons. At the deep end of the ecogradient, LBF delay reproduction and grow longer. Large juveniles (with much symbiont-rich protoplasm) are favored under these low light conditions. Such populations are under stress-selection. At the shallow end of the range, reproduction is also delayed (to increase either fecundity or juvenile size because of low juvenile survival in high energy conditions), but because of the optimality of the environment (*i.e.*, low stress), growth rate is normal or even accelerated. These populations are under *K*-selection. Environmental variables exert a direct influence on the life history and development of larger foraminifera. By delaying reproduction (hypermorphosis) to increase fecundity or juvenile size at the extremes of a species' range, larger intraspecific body sizes result.

II. INTRODUCTION

The relationship of heterochrony (changes in the rates and/or timing of ontogenetic processes) to life history strategies has been developed in the context of *r* and *K* selection. As summarized by McKinney and McNamara (1991, p. 268), *r*-selected populations normally inhabit highly fluctuating environments with unpredictable resources, whereas *K*-selected populations are typical of stable, crowded (*i.e.*, competitive) environments. Some life history attributes of *r*-selected organisms might include small size, early sexual maturation, semelparity, large reproductive allocation, and high numbers of small offspring. *K*-selected organisms are frequently characterized by large size, delayed sexual maturation, iteroparity, low reproductive allocation, and few, large offspring. The *r*-*K* concept represents a continuum of life history strategies. Al-

though the generality (and even validity) of the *r-K* model has been contested, it remains a useful concept (see Boyce, 1984).

As summarized by Gould (1977, p. 289-294), one of the most important life history attributes in *r-K* selection theory is the timing of reproduction. Given the primacy of reproductive timing, specific heterochronic processes would be expected to be associated with *r* and *K* strategies. Under conditions of *r*-selection, *progenesis* (early onset of sexual maturity) and *acceleration* (increased rate of development) should be common. Under conditions of *K*-selection, *hypermorphosis* (delayed onset of sexual maturity), and *neoteny* (reduced rate of development) are expected (McKinney and McNamara, 1991, p. 269).

A recent expansion of the *r-K* model has been the addition of a third end-member to the *r-K* continuum: stress ("stress adaptation" or "stress tolerance": McKinney and McNamara, 1991). Stress-selection occurs in environments that are persistently suboptimal for normal growth and function. According to Grime (1989, p.4), stress is defined as "external constraints limiting the rates of resource acquisition and growth or reproduction of organisms." For marine invertebrates, stress may include (Hallam, 1965) extremes in temperature or salinity, water turbidity and motion, nutrient and oxygen availability, organic content of substrate, solar radiation (especially for organisms harboring photosynthetic symbionts), and crowding.

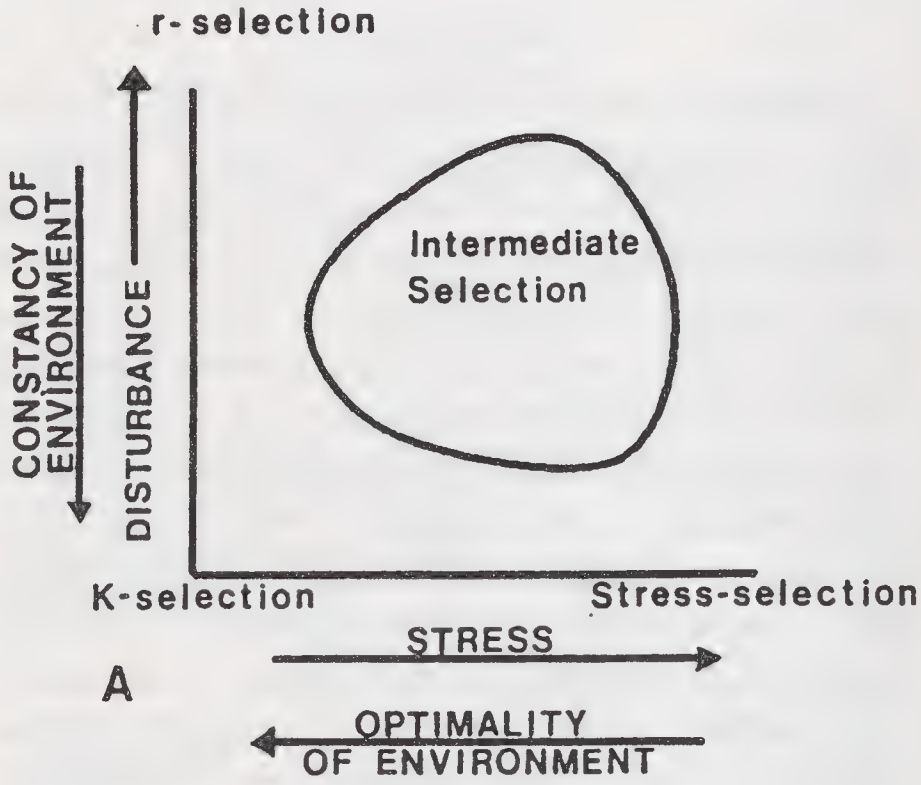
McKinney and McNamara (1991, p. 377) relate stress-selection to the *r-K* model as follows:

> "Whereas *r*- and *K*-selection represent extreme poles of an axis of environmental stability (disturbance frequency), *K*- and stress-selection represent extreme poles of an axis of environmental stress (or optimality). In other words, any environment on this latter axis is predictable (stable, generally constant), but it may be predictably suboptimal for one or more parameters."

Furthermore, *K*-selection is a density-dependent natural selection (Boyce, 1984), and promotes life history characteristics in response to competition, predation, and other density-dependent pressures. Although high density may be a form of stress, stress-selection encompasses a number of other factors and may occur irrespective of population density or competition. In terms of heterochronic responses to stress, stress-selected species (just as *K*-selected species) would be expected to delay reproduction (hypermorphosis) and to grow more slowly (neoteny). The relationships between environmental disturbance and stability, *r*- *K*- and stress-selection, and the predicted heterochronic processes are illustrated in Figure 1.

The Biology of Larger Benthic Foraminifera

Larger benthic foraminifera (herein LBF) is an informal designation for numerous taxa that typically reach more than three cubic mm in test volume and have



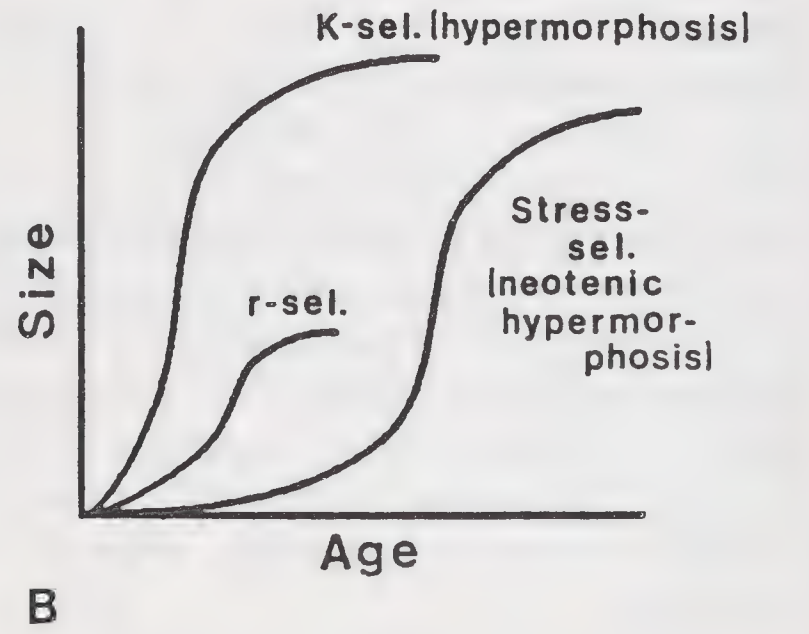


Figure 1. The relations between *r*-, *K*-, and stress-selection and ontogeny. *A.*, *r*-, *K*-, and stress-selection as three end-members along two gradients, disturbance frequency and stress (optimality). *B.*, Predicted ontogenetic curves favored by the three kinds of selection (from McKinney and McNamara, 1991, p. 379, figure 9-4).

complex internal morphologies (most foraminiferans do not exceed 1-2 mm in size: Lee and Hallock, 1987; Hallock, 1985; Ross, 1974). Algal symbiosis has been demonstrated for most modern species of LBF (symbionts include chlorophytes, rhodophytes, diatoms, and dinoflagellates: Leutenegger, 1984; Lee and Anderson, 1991), and it is generally thought that large test size is somehow related to symbiosis (which may facilitate calcification, for example; see Cowen, 1983). Likewise, the complexity of the LBF test may be, in part, a function of cytoplasmic compartmentalization and specialization (such as the housing and sheltering of symbionts in regions of optimal illumination, and away from cytoplasmic flow: Lee and Hallock, 1987; Leutenegger, 1984).

Larger foraminifera are found primarily in tropical to subtropical, oligotrophic environments. They are especially prominent in coral reefs and related facies and can be substantial sediment producers, rivaling corals and calcareous algae in their volumetric contribution (Hallock and Glenn, 1986; Hallock, 1981a; Ross, 1977). Most extinct LBF are associated with similar paleoenvironments, and are inferred to have had algal symbionts (Hallock, 1982).

Foraminifera have extremely variable life cycles (see Lee and Capriulo, 1990), which can extend up to one year or more (Ross, 1974; Lutze and Wefer, 1980). Most larger foraminifera are characterized by an alternation of generations in which a haploid *gamont* (gamete-producing) form (also called the A-generation) alternates with a diploid *agamont* (asexual) form (also called a *schizont*, or B-generation). This heterophasic life cycle frequently results in both morphologic and nuclear dimorphism. The gamont normally has a smaller test than the agamont. The agamont, however, is typically multinucleate (heterokaryotic), with one or more macronuclei controlling somatic and metabolic functions, and many micronuclei that divide to produce nuclei during schizogony (macronuclei degenerate during reproduction).

Morphologic dimorphism of the foram test is also apparent in the embryonic chambers (embryon) of both gamont and agamont. The embryon of the gamont normally consists of two large chambers (protoconch and deuteroconch; or proloculus and deuteroloculus, if part of a primary spire), and is termed *megalospheric*. These two initial chambers house the juvenile foraminiferan when first released from the parent test during asexual reproduction. The agamont, formed by the fusion of gametes, has an extremely small initial chamber (proloculus), and is termed *microspheric* (Loeblich and Tappan, 1964; Lipps, 1982).

Morphologic dimorphism in test size can be extreme in larger foraminifera, with the adult microspheric form reaching several times the size of the megalosphere. In the Permian, some fusulinid microspheres (genus *Parafusulina*) reached 10 cm in length (Dunbar, 1963), and I have verbal reports of microspheric individuals of Tertiary *Nummulites* from the Middle East reaching 12 cm in diameter (B. Carter, pers. comm.). Some fragments of *Lepidocyclina* found in the course of this study represent individuals which must have approached 7 cm or more in diameter.

In both living and fossil assemblages, microspheric individuals are typically very uncommon. Megalospheres are always disproportionally greater in number. This has led to the hypothesis of biologic trimorphism, in which it is thought that microspheric schizonts produce megalospheric schizonts, which produce megalospheric gamonts, which produce microspheric schizonts (Leutenegger, 1977). Several generations, in fact, of megalospheric schizonts are thought to precede gametogenesis in some cases. Although this theory has been disputed in the past (Rottger *et al.*, 1986), it has recently been confirmed for *Heterostegina depressa* (Rottger *et al.*, 1990).

The Ecological Significance of Test Size in Larger Foraminifera

The complexity of the LBF test records a wealth of biological information (Hottinger, 1978, 1986). However, there are three aspects of LBF test size which make it an especially useful indicator of development and reproductive strategy.

First, like most lower invertebrates, LBF have indeterminate growth. As summarized by Hallock and Glenn (1986), under favorable conditions, LBF will mature and reproduce at relatively small sizes. However, if the population is stressed by low light (necessary for symbionts),

low temperature, or other suboptimal conditions, the forams will delay reproduction and simply continue to grow. This is observed, for example, when shallow-dwelling forms are washed into deep water. Ironically, if a population contains many large individuals, conditions for growth and reproduction may have been marginal. *Within a species, test size is generally a reliable relative indicator of individual age.*

Second, LBF are semelparous. That is, during multiple fission, the entire protoplasm of the adult foram is divided among its progeny. Reproduction is a major cause of mortality among adults (Hallock, 1985; Hallock and Glenn, 1986; Hallock *et al.*, 1986). *If the adult size distribution of a population is unimodal, the size at reproduction is approximated by the peak of the curve.* This, of course, assumes that taphonomic processes have not significantly altered the assemblage.

Third, because LBF distribute all of their protoplasm to juveniles during asexual reproduction, test size is a good indicator of reproductive allocation. LBF fecundity (the number of offspring produced by a parent during asexual reproduction) is a function of test size (Hallock, 1985; Hallock *et al.*, 1986). *LBF fecundity is normally directly proportional to body size.*

In addition, the LBF megalospheric embryon (first two chambers of the LBF test) represents the juvenile foram when it was first released from the parent test. *Embryon size indicates the size of the individual foram at birth.* This can be of special significance in the study of LBF life history. Survival rates are typically very low for juvenile LBF. However, if juveniles can survive to a certain critical size (0.5 mm for extant *Amphistegina*), chances of survival to reproduction are greatly increased (Hallock, 1985). Survival is largely size-specific.

Theoretical Predictions for Fossil Larger Foraminifera

Paleontologists working on LBF have long known of the incredible amount of morphologic variation in the group (see Frost and Langenheim, 1974, p. 43). In the past, this variation, plus the desire to use LBF for biostratigraphic purposes, resulted in an excessive proliferation of taxonomic names. Fortunately, most of these names have been relegated to synonymies. This is notably true for American species, where diversity is actually quite low compared to Tethyan and Indo-Pacific faunas (particularly in the Oligocene). Few investigators, however, have tried to make ecological sense of this variability.

The initial aim of this investigation was to examine the morphological (developmental) and life history adaptations of four species of LBF along a paleoenvironmental transect in Lower Oligocene carbonates of the eastern Gulf Coastal Plain. In particular, mean adult *test size* and *embryon size* were examined.

The fossil LBF used were taken along a shallow reef-to-deep forereef and shelf paleoenvironmental gradient and are assumed to have lived under progressively less disturbed and less illuminated conditions. From the outset of this study, the following morphologic patterns were expected to be found along this paleodepth gradient:

(1) *Mean population test size should increase with depth.* This is a function of reduced solar illumination and temperature, making conditions suboptimal for growth and reproduction. But because of their indeterminate growth, by delaying reproduction the LBF grow to larger sizes. At greater depths, metabolism and growth are necessarily slowed. As Hallock (1985) has shown in her models for LBF adaptive strategies, both low juvenile growth rates and low juvenile survival favor large adult size and high fecundity. A corollary of this prediction is that the amount of post-embryonic growth (measured by equatorial chamber area) should also increase with depth.

(2) *Embryon size should increase with depth.* Increase in embryon size commonly (but by no means always) accompanies increase in test size in LBF. According to Hallock (1985), an increase in embryon size increases the chances of juvenile survival, which is typically very low in LBF. In explaining observed patterns of increasing embryon size with depth in fossil *Discocyclina,* for example, Hallock suggests that larger embryons receive more protoplasmic symbionts from the parent, thus increasing chances of survival under conditions of low light penetration. It is clear that there may be many reasons for

changes in embryon size, not all of which are understood (Drooger, 1983; and Discussion section below). As the results of the present investigation confirm, embryon size must be interpreted cautiously.

(3) *Test elaborations (such as development of pillars and pustules), selliform tests, and a decrease in length/width ratios (nummulitids) should be more common in shallow, high energy conditions.* It has been documented for both fossil and extant LBF that certain test modifications are commonly associated with high energy conditions. These are presumably adaptations for test strength, and reflect high calcification rates. Pillars, for example, (radial thickenings extending from the center of lepidocyclinid tests, manifested by rounded prominences called pustules on the test centrum) are common in high energy facies (Drooger, 1983; Frost and Langenheim, 1974, p.135-136). Selliform ("saddle-shaped") tests have been recorded for reef-dwelling populations of *Lepidocyclina undosa* from Mexico (Frost and Langenheim, 1974, p. 170). And test flattening is commonly observed as a correlate with depth (low energy) in a variety of LBF (Reiss and Hottinger, 1984; Hallock, 1979).

III. METHODS

Field and Laboratory Work

Larger foraminifera were collected (Fig. 2) during the course of field work for a regional facies analysis of Lower Oligocene strata of the eastern Gulf Coast (Bryan, 1991, 1993). Bulk samples were collected for preparation in the laboratory. Samples used include the Bridgeboro Limestone type section (Bridgeboro, Georgia); Duncan Church Beds of the Bridgeboro Limestone (Wausau, Florida); Florala Limestone (Florala, Alabama); Glendon Limestone (Jackson, Alabama); and the Marianna Limestone (Jackson, Alabama).

The diagnostic morphologic features of larger foraminifera (such as embryonic and equatorial chambers) are found *within* the test, requiring that the test be partially destroyed before measurements can be taken. Most specimens cannot be identified with certainty without such preparation. Preparation of lepidocyclinids requires that the each specimen be mounted (with resin) to a 1x3" glass slide, then ground on a frosted glass plate (as with a thin section) until the equatorial plane and embryonic chambers of the foram are in full view. Nummulitids can be split across their equatorial plane of weakness (the marginal cord) by heating the specimen over an alcohol lamp, then plunging the specimen in water. These methods are elaborated in Bryan (1991). Over 1000 individual specimens were prepared for this study.

Cross-sectional area measurements (used as a proxy for embryon volume) of nummulited and lepidocyclinid embryons were made with the aid of a digitizing tablet, binocular microscope, video camera and monitor, computer, and JAVA (Jandel

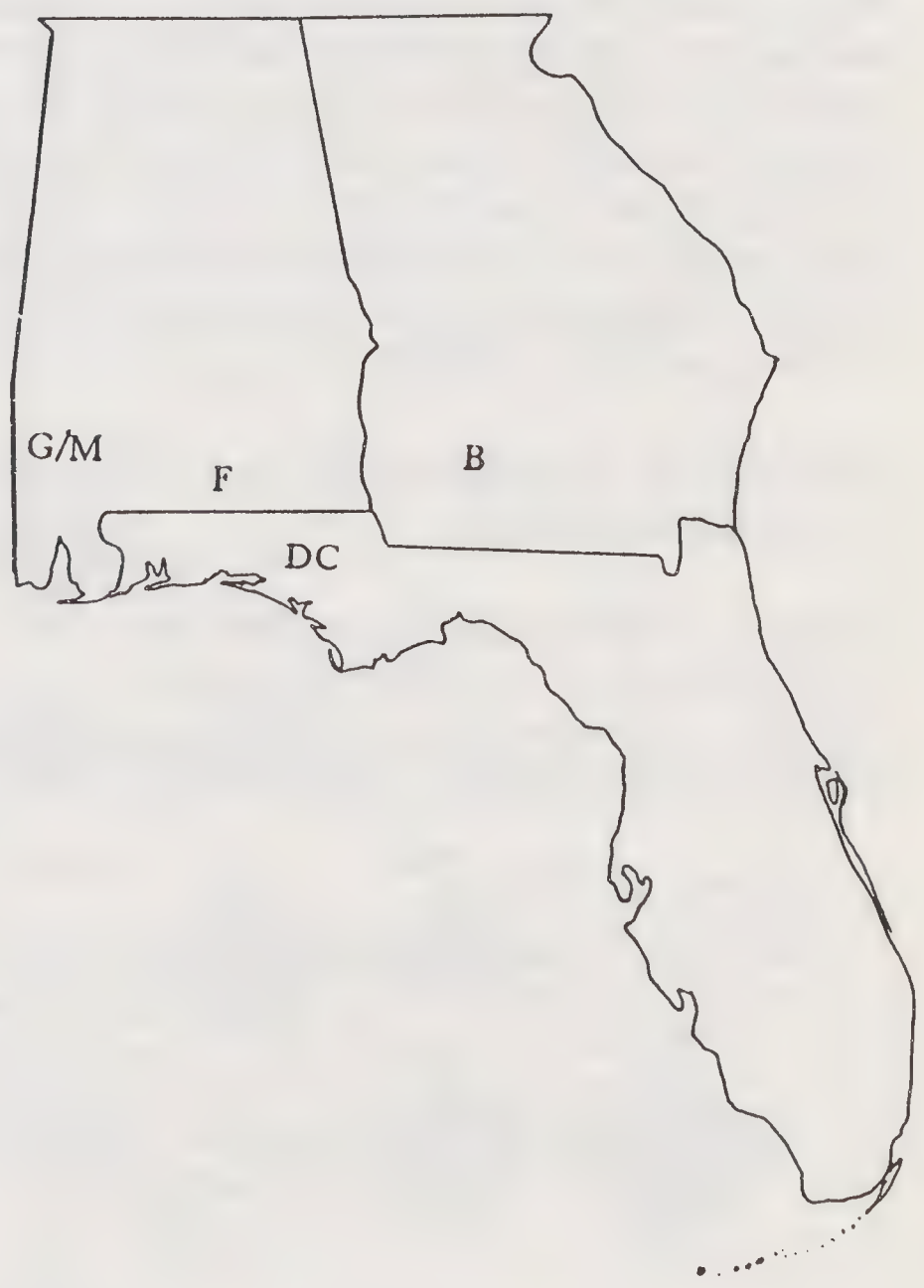


Figure 2. Locality map, eastern Gulf Coastal Plain. *G/M*, Glendon and Marianna Limestones as exposed at the St. Stephens Quarry, Washington County, Alabama; *F*, Florala Limestone type section, Covington County, Alabama; *DC*, Duncan Church Beds of the Bridgeboro Limestone, Washington County, Florida; *B*, Bridgeboro Limestone type section, Mitchell County, Georgia.

Video Analysis) biometric software package. Test diameters were measured with a digital caliper. The amount of post-embryonic, equatorial growth was calculated for lepidocyclinids, and various qualitative features (*e.g.*, presence or absence of pustules) were also taken into account (Bryan, 1991).

Larger Foraminifera Examined

Four species of LBF were examined. *Nummulites (Paleonummulites) panamensis* Cushman is the only nummulitid found in the Lower Oligocene of the eastern Gulf Coast, and is widespread in the Caribbean. Three lepidocyclinids were examined: *Lepidocylina (Lepidocyclina) mantelli* (Morton), a form common in Oligocene to Lower Miocene strata of the Gulf Coast and Caribbean; *Lepidocylina (Neprolepidina) yurnagunensis* Cushman, also common from the Oligocene to Lower Miocene in the Gulf Coast and Caribbean; and *Lepidocylina (Eulepidina) undosa* Cushman, considered a standard index species for the Oligocene of the Americas (Frost and Langenheim, 1974).

Synopsis of Stratigraphic and Paleoenvironmental Setting

Before paleobiological questions could be addressed, it was first necessary to establish a paleoenvironmental framework through facies analysis (independent of environmental inferences drawn from LBF). The interval chosen is a portion of the Vicksburgian (Lower Oligocene) section of the eastern Gulf Coastal Plain, containing LBF-rich carbonates. A full stratigraphic and paleoenvironmental analysis of this time interval is given Bryan (1991, 1993). The units used are correlative both lithostratigraphically and biostratigraphically (with the exception of the Marianna Limestone), and represent a series of laterally adjacent paleoenvironments.

The forams used in this study are from the Bridgeboro Limestone (type section), the Duncan Church beds of the Bridgeboro Limestone, the Florala Limestone, the Glendon Limestone, and the Marianna Limestone. These formations represent a transect across an extensive carbonate platform and shelf in the Gulf Coast during Lower Oligocene time. In summary, the paleoenvironments represented by this transect are: (1) coralgal shelf margin (platform-like) buildup (Bridgeboro type section), which flanked the Gulf Trough (a narrow current-swept channel stretching from panhandle Florida to central Georgia); (2) forereef coralgal limestone (Duncan Church beds, Bridgeboro Limestone); (3) deep forereef, platey coralgal limestone (Florala Limestone); (4) deep, shelf margin (ramp) bank grainstone (Glendon Limestone); and (5) mid-to outer shelf carbonate mudstone (Marianna Limestone). These facies are illustrated in the block diagram model of Figure 3.

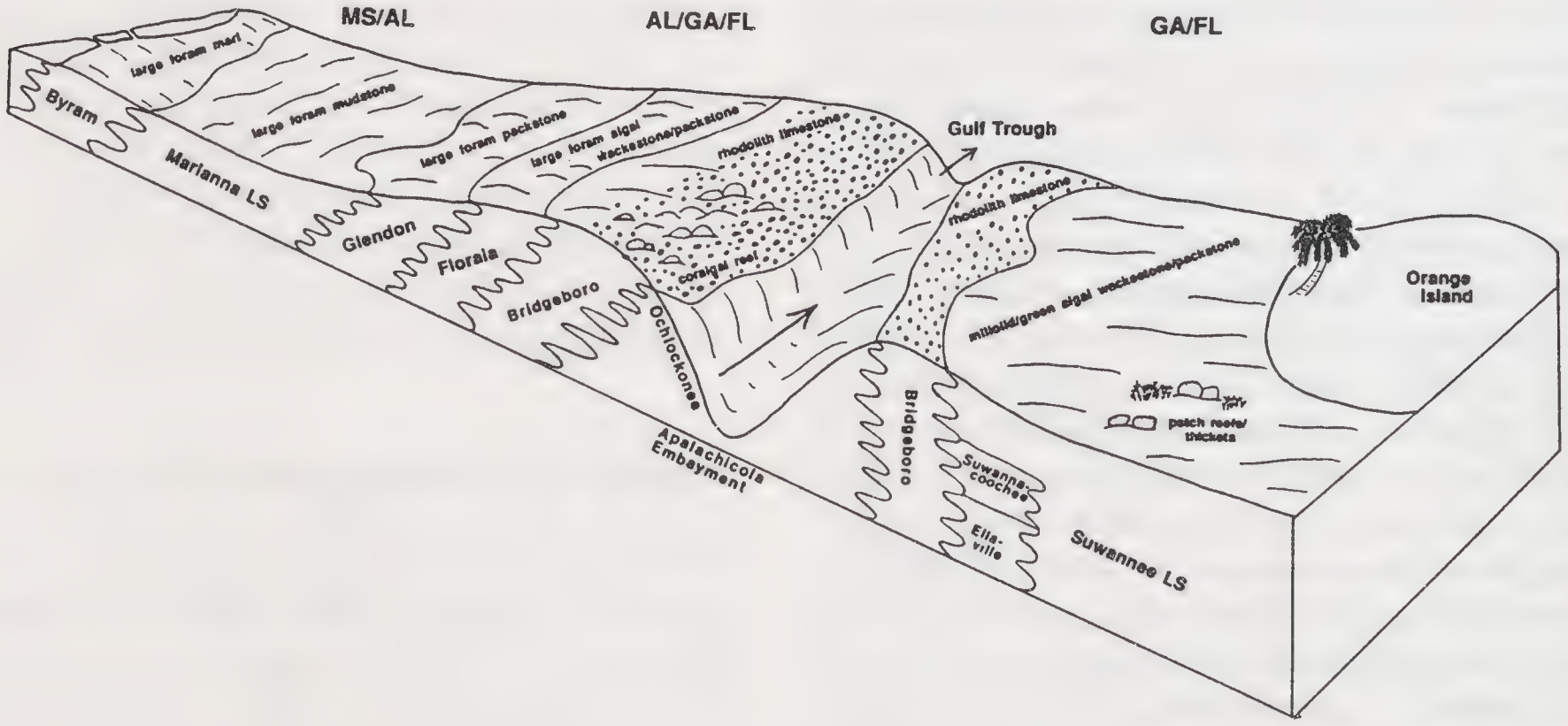


Figure 3. Block diagram reconstruction of Vicksburgian carbonate facies across the eastern Gulf Coastal Plain (from Bryan, 1991, 1993).

The lateral gradation of Bridgeboro–Duncan Church–Florala–Glendon–Marianna, represents progressively deeper paleoenvironments. The best evidence for this deepening is the local presence of massive reef corals and changes in coralline algal morphology (see Steneck, 1986). In short, the type section of the Bridgeboro contains reef corals and extensive formations of large, well-rounded rhodoliths in a grainstone matrix. The Duncan Church beds of the Bridgeboro Limestone contain only small, sub-rounded rhodoliths and algal marls. The Florala Limestone contains extensive, thin, platey red algae in a mudstone matrix. The glauconite-rich Glendon Limestone has only rare algal marls. The muddy Marianna Limestone contains no algal remains.

IV. RESULTS

Distributional and Biometric Trends

The facies distribution and relative abundance of the four LBF species are illustrated in Figure 4 and are based on the data of Table 1. From this figure, a shallow-to-deep water gradient in LBF species composition is clearly evident, and this biofacies pattern is consistent with previous reports (such as Frost and Langenheim, 1974). Biometric results are presented in Tables 2-5.

Nummulites panamensis (Table 2, Figs. 5, 6) is found almost exclusively in the Glendon and Florala Limestones. Test diameter, test width, and embryon size are significantly greater in the shallower water Florala sample. The average diameter/width ratio, however, is greater in the Glendon assemblage (3.58) than in the Florala (2.44). These observations are consistent with those of Frost and Langenheim (1974, p. 84-89) on Mexican *N. panamensis*, where compressed forms with smaller proloculi are more common in deeper water facies. The Florala assemblage also has a slightly higher percentage of microspheric specimens (2.2%) than does the Glendon (1%). Unfortunately, the limited occurrence of *N. panamensis* in only two of the formations examined makes the recognition of morphologic trends difficult.

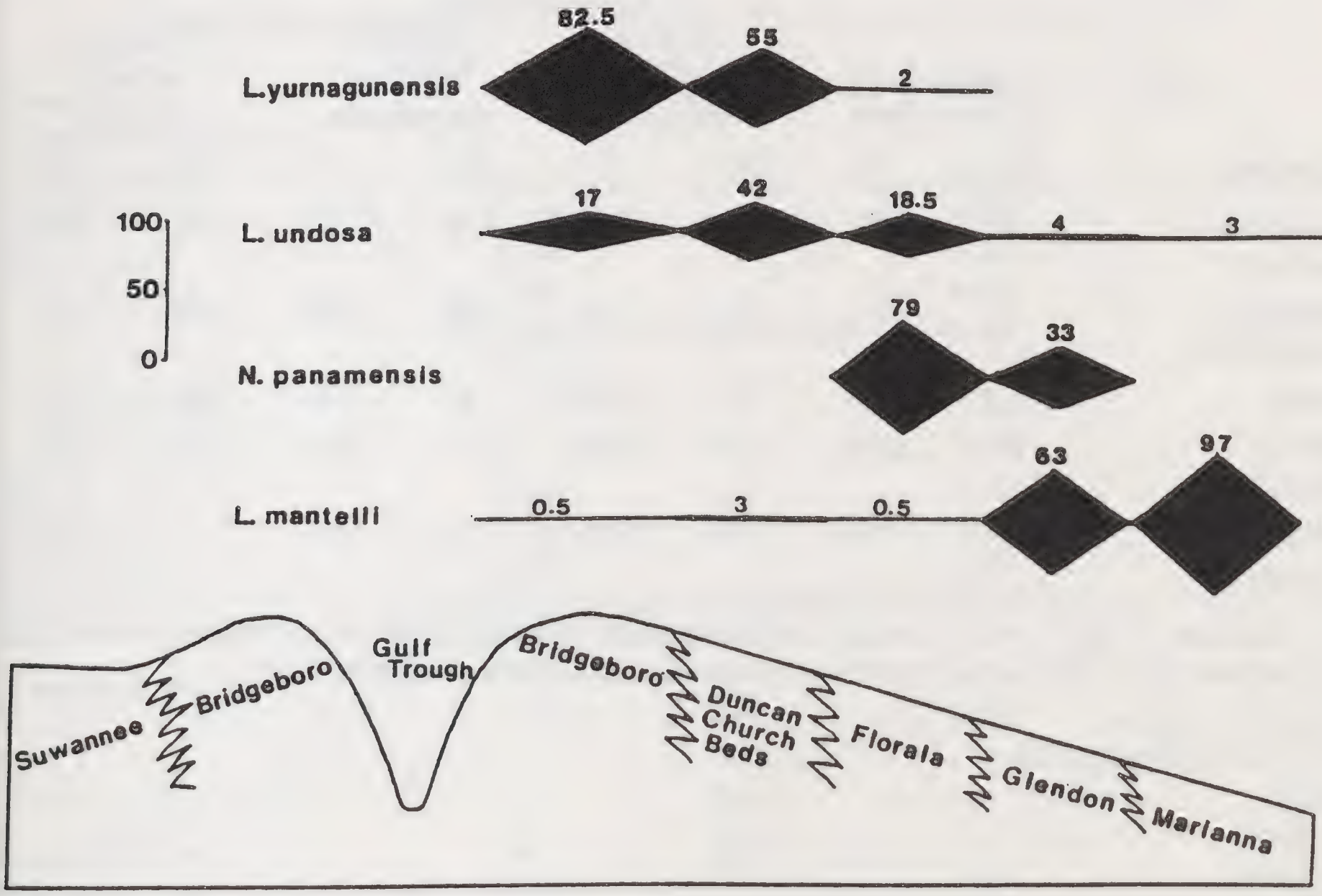


Figure 4. Spindle diagram showing facies distribution, absolute abundance, and percentage abundance of larger foraminifera taxa in the study area. Vertical scale on left for absolute abundances shown by vertical height of diamonds.

Lepidocyclina (Lepidocyclina) mantelli (Table 3, Figs. 4, 5, 6, 7) is found in all five facies, but is common only in the Glendon and Marianna Limestones. The assemblage from the deeper water wackestones of the Marianna shows significantly larger mean test size, embryon size, and post-embryon size. The Marianna assemblage also has a slightly higher percentage of microspheric specimens (8%) than does the Glendon (5.5%). Although much rarer in the Florala, Duncan Church, and Bridgeboro samples, *L. mantelli* generally has larger test size, embryon size, and post-embryon size in these facies.

Lepidocyclina (Nephrolepidina) yurnagunensis (Table 4, Figs. 4, 5, 6, 7) is found in great abundance in the Bridgeboro Limestone type section and the Duncan Church beds, and is present in fewer numbers in the Florala Limestone. Test size and post-embryon size are greatest in the Bridgeboro type section, smaller in the Duncan Church beds, and return to a larger sizes in the Florala. Microspheric specimens were found only in the Bridgeboro type section (1.7% of the assemblage). Embryon size is greatest in the Bridgeboro type section, and decreases in the Duncan Church and Florala. In the Bridgeboro type section, *L. yurnagunensis* almost always has pustules on the centrum, a feature commonly displayed by this species in high energy environments and sometimes designated by the subspecies name *morganopsis*. Specimens from the lower energy Duncan Church beds do not have pustules, and fit the description of the subspecies *yurnagunensis* (Frost and Langenheim, 1974). Pustulose and non-pustulose *L. yurnagunensis* are associated with high-energy biosparites/patch reefs and lower-energy, forereef slope biomicrites (respectively) in the Oligocene of Ja-

Table 1

Number of Specimens and Percentage Abundances of Larger Foraminifera from the Marianna, Glendon, Florala, and Bridgeboro Limestones

	Nummulites panamensis		*Lepidocyclina (Lepidocyclina) mantelli*		*Lepidocyclina (Nephrolepidina) yurnagun.*		*Lepidocyclina (Eulepidina) undosa*	
Formation:	No.	%	No.	%	No.	%	No.	%
Bridgeboro (type sect.)	0	0%	1	0.5%	174	82.5%	36	17%
Bridgeboro (Duncan Ch.)	0	0%	8	3%	168	55%	129	42%
Florala	410	79%	3	0.5%	9	2%	96	18.5
Glendon (St.Steph.)	94	33%	179	63%	0	0%	10	4%
Marianna (St.Steph.)	0	0%	100	97%	0	0%	3	3%

Total number of specimens picked per formation sample, used to calculate percentage abundances (does not include microspheres nor unidentified specimens):

Bridgeboro (type)	211
Bridgeboro (Duncan Ch.)	305
Florala*	518
Glendon	283
Marianna	103

*The original Florala Sample had 144 lepidocyclinids and 447 nummulites (=591 total). Of these, 37 lepidocyclines were unidentifiable. Therefore, 37 nummulites were subtracted from 447 (=410) for percentage calculations. (Also, the nummulite sample was split twice before a reasonable working size was obtained).

maica and Mexico (Frost and Langenheim, 1974).

Lepidocyclina (Eulepidina) undosa (Table 5, Figs. 4, 5, 6, 7) is common in the Bridgeboro type section, Duncan Church beds of the Bridgeboro, and Florala Limestone, and is found more rarely in the Glendon and Marianna Limestones. Test size, embryon size, and post-embryon size generally increase towards the Bridgeboro reef facies and decrease towards the Glendon, but radically rise again in the deep-water Marianna Limestone (although few specimens are present). Frost and Langenheim (1974, p.170-172) report that Mexican populations of *L. undosa* in shallow, high-energy reef deposits also have larger embryonic chambers than those from lower energy facies. Although *L. undosa* is frequently reported to have selliform tests (especially in reef facies), there was no evident trend of more abundant selliform tests in the Bridgeboro. Microspheric specimens are generally rare, except in the Duncan Church beds, where they compose 9.3% of the assemblage.

Potential Taphonomic Bias

A potential source of bias in this study is taphonomic alteration, particularly in high energy facies or areas of reduced sedimentation. Facies with fine grain size would predictably be less altered. While taphonomic studies of fossil LBF are not common, analysis of some modern LBF living and dead assemblages indicates that thanatocoenoses often faithfully represent the biocoenoses (Jell *et al.*, 1965; Zohary *et al.*, 1980; Reiss and Hottinger, 1984, p. 15). Nevertheless, abrasion, bioerosion, dissolution, and transport can alter assemblages (Martin and Liddell, 1991).

In high energy facies, larger sized LBF may be preferentially preserved. In the Bridgeboro Limestone (the highest energy facies) small individuals were abundant, and there is no indication of differential preservation. The same is true of all facies studied. It is concluded, therefore, that taphonomic effects have not significantly altered the assemblages. This is certainly an oversimplification, but there are no ob-

Table 2

Biometric Statistics for *Nummulites (Paleonummulites) panamensis*

Locality:	Glendon Limestone	Florala Limestone
Test Diameter (mm)		
Sample Size	96	92
Mean	1.62	1.97
Std. Dev.	0.56	0.49
Coef. Var.	0.35	0.25
t-test	t = 4.52; means are different at 0.05 level	
Test Width (mm)		
Sample Size	21	92
Mean	0.54	0.83
Std. Dev.	0.17	0.23
Coef. Var.	0.31	0.27
t-test	t = 5.47; means are different at 0.05 level	
Diameter/Width Ratio	3.58	2.44
Embryon Size (mm^2)		
Sample Size	25	75
Mean	0.01	0.02
Std. Dev.	0.001	0.02
Coef. Var.	0.14	1.0
t-test	t = 3.06; means are different at 0.05 level	

vious indications of size-sorting, at least. Still, many LBF examined in this study show signs of rounding and abrasion. Additional work on the distribution of such features (within an assemblage and across different facies) would sort out this potential source of bias.

V. DISCUSSION

A New Hypothesis

At the outset of this investigation, it was expected that both test size and embryon size would increase in deeper water facies (Fig. 8). However, this prediction was met only in part. What was not anticipated was an increase in test and embryon size as the reef (Bridgeboro Limestone) is approached. This pattern is common in *L. undosa*, *L. yurnagunensis*, and *N. panamensis* (Figs. 5, 6, 7). This discovery led to a reconsideration and expansion of the original hypotheses.

As summarized by Hallock (1985), large test size and large embryon size may essentially be adaptations for conditions of low juvenile survival. But such conditions may be found in a variety of environments, and for as many reasons. My initial premise of increasing test size and embryon size with increasing depth was too simplistic. While increased depth may indeed be unfavorable for juvenile survival (because of reduced illumination for symbionts in nutrient-poor waters), extremely shallow

Table 3

Biometric Statistics for *Lepidocyclina (Lepidocyclina) mantelli*

Locality:	Marianna Limestone	Glendon Limestone	Florala Limestone	Bridgeboro Limestone (Duncan Ch)
Test Diameter (mm)				
Sample Size	61	95	3	7
Mean	5.80	2.74	4.75	3.77
Std. Dev.	2.49	1.61	0.76	1.39
Coef. Var.	0.43	0.58	0.16	0.37
t-test:				
Mar/Glen: t = -4.32; means are different at 0.05 level				
Mar/Bbro: t = 2.11; means are different at 0.05 level				
Glen/Bbro: t = -1.64; means are not different at 0.05 level				
Embryon Size (mm^2)				
Sample Size	61	95	3	7
Mean	0.46	0.19	0.27	0.33
Std. Dev.	0.12	0.09	0.10	0.11
Coef. Var.	0.26	0.47	0.37	0.33
t-test:				
Mar/Glen: t = -17; means are different at 0.05 level				
Mar/Bbro: t = -.0029; means are different at 0.05 level				
Glen/Bbro: t = 4.15; means are different at 0.05 level				
Post-Embryonic Growth (mm^2)				
Sample Size	61	95	3	7
Mean	30.86	7.72	17.76	12.11
Std. Dev.	24.58	10.57	5.45	7.16
Coef. Var.	0.79	1.36	0.31	0.59
t-test:				
Mar/Glen: t = -0.809; means are different at 0.05 level				
Mar/Bbro: t = 1.99; means are different at 0.05 level				
Glen/Bbro: t = -1.07; means are not different at 0.05 level				

conditions, such as on a reef, may be equally unfavorable. As Hallock (1985) has found experimentally, juveniles of *Amphistegina* less than 0.5 mm in size can be dislodged from their substrate with even gentle water motion. Large embryon size may be favored in shallow, high energy conditions because too small juveniles are at risk of being dislodged from their substrate. But in deep waters, small juveniles may have insufficient protoplasmic symbionts to survive in low light conditions.

Unfortunately, previous studies do not show a consistent correlation between individual test size and embryon size. Depth-related trends have been found in some LBF, but this is not a consistent pattern (Drooger, 1983). Furthermore, it has not been established whether larger parents produce more juveniles of the same size, or fewer, larger embryons. While the former is possible, it is unlikely that increasing embryon size would proceed without some increase in adult size (Hallock, 1985). In short, the ecological significance of embryon size is not easily evaluated. Nevertheless, following the models developed by Hallock (1985), increasing test size increases individual fecundity, and is a response to high juvenile mortality. Under conditions of low juvenile survival, LBF may only be able to respond by increasing fecundity or increasing embryon size. And both strategies could occur in the same environment.

In this investigation, test size was generally found to increase in both the shallow and deeper extremes of the ranges of three out of four species (Fig. 5). Embryon size appears to show this same pattern in two of the four species (Fig. 6), but the statistical significance of this pattern is equivocal. None of the species contradicts either pattern. These data, in combination with the model of Hallock (1985), are combined to

Table 4

Biometric Statistics for *Lepidocyclina (Nephrolepidina) yurnagunensis*

Locality:	Florala Limestone	Bridgeboro Limestone (Duncan Church)	Bridgeboro Limestone (Type Section)
Test Diameter (mm)			
Sample Size	9	167	174
Mean	2.46	1.90	3.04
Std. Dev.	0.38	0.57	1.04
Coef. Var.	0.15	0.30	0.34
t-test:			
DCh/Bbro: t = 1.25; means are different at 0.05 level			
Embryon Size (mm^2)			
Sample Size	8	130	153
Mean	0.05	0.062	0.088
Std. Dev.	0.02	0.025	0.081
Coef. Var.	0.40	0.42	0.88
t-test:			
DCh/Bbro: t = 3.61; means are different at 0.05 level			
Post-Embryonic Growth (mm^2)			
Sample Size	8	131	153
Mean	4.72	2.98	7.91
Std. Dev.	1.49	1.67	5.08
Coef. Var.	0.32	0.56	0.64
t-test:			
DCh/Bbro: t = 1.06; means are different at 0.05 level			

generate a new hypothesis to predict test size and embryon size in LBF along a shallow, high energy to deep, low energy environmental gradient:

> If a species extends along a sufficient range across a shallow, high energy, high illumination-to deep, low energy, low illumination ecogradient, it is predicted that test size and embryon size will generally be larger at the extremes of this range (Fig. 9).

Shallow, high energy/well-illuminated conditions favor large adult size and larger juveniles, which can avoid being easily dislodged from their substrate (increased fecundity is another possible ecologic strategy and correlate of large size). Deep,

Table 5
Biometric Statistics for *Lepidocyclina (Eulepidina) undosa*

Locality:	Marianna Limestone	Glendon Limestone	Florala Limestone	Bridgeboro Limestone (Duncan Church)	Bridgeboro Limestone (Type Section)
Test Diameter (mm)					
Sample Size	2	10	93	128	31
Mean	7.88	3.53	3.55	5.42	5.84
Std. Dev.	4.90	2.56	1.82	3.54	2.50
Coef. Var.	0.62	0.73	0.51	0.65	0.43
t-test:					
Glen/Flo: t = -0.042; means are not different at 0.05 level					
Glen/DCh: t = 1.65; means are not different at 0.05 level					
Glen/Bbro: t = -2.53; means are different at 0.05 level					
Flo/DCh: t = 4.65; means are different at 0.05 level					
Flo/Bbro: t = -5.50; means are different at 0.05 level					
DCh/Bbro: t = 0.63; means are not different at 0.05 level					
Embryon Size (mm^2)					
Sample Size	2	10	89	99	31
Mean	0.76	0.49	0.53	0.65	0.48
Std. Dev.	0.19	0.22	0.29	0.20	0.15
Coef. Var.	0.25	0.45	0.55	0.31	0.31
t-test:					
Glen/Flo: t = 0.46; means are not different at 0.05 level					
Glen/DCh: t = -2.39; means are different at 0.05 level					
Glen/Bbro: t = -0.15; means are not different at 0.05 level					
Flo/DCh: t = -3.29; means are different at 0.05 level					
Flo/Bbro: t = -0.97; means are not different at 0.05 level					
DCh/Bbro: t = -4.36; means are different at 0.05 level					
Post-Embryonic Growth (mm^2)					
Sample Size	2	10	89	99	31
Mean	57.37	13.90	11.85	19.83	31.09
Std. Dev.	60.81	20.56	12.88	18.08	25.97
Coef. Var.	1.06	1.48	1.08	0.91	0.83
t-test:					
Glen/Flo: t = 0.45; means are not different at 0.05 level					
Glen/DCh: t = 0.098; means are not different at 0.05 level					
Glen/Bbro: t = -1.90; means are not different at 0.05 level					
Flo/DCh: t = 3.45; means are different at 0.05 level					
Flo/Bbro: t = -5.37; means are different at 0.05 level					
DCh/Bbro: t = -2.70; means are different at 0.05 level					

low energy/low light conditions also favor large adult size and large juveniles, which inherit many symbionts from the parent test (necessary in low light conditions). Thus, large test and embryon size are predicted at the limits of a species' range, but for different reasons. Smaller test and embryon sizes will be expected in intermediate areas that favor reproduction in minimal time.

Some comments regarding these generalities must be given here. First, this prediction is for intraspecific variability. Interspecific patterns may show different features. *Lepidocyclina yurnagunensis* and *L. undosa,* for example, are both common in the Bridgeboro Limestone, but *L. undosa* is a much larger species than *L. yurnagunensis* in both test and embryon size. *Lepidocyclina yurnagunensis* almost certainly had a different reproductive schedule and potential rate of population increase than did *L. undosa.*

A problem with testing the revised hypothesis is that many species appear to have a limited range. *Lepidocyclina mantelli,* for example, is restricted to relatively deep shelf areas (although it occurs in low numbers in other facies), while *L. yurnagunensis* is primarily a reef dweller (Fig. 4). Such limited ranges may in part reflect host-specific adaptations of symbionts. As shown by Leutenegger (1984) for some modern LBF, hosts with chlorophycean symbionts are restricted to shallow water, those with dinophyceans or rhodophyceans occur between 0-70 meters depth, and LBF with diatom symbionts extend from 1-130 meters depth.

Further testing of the revised hypothesis here would require a finer-scale sampling scheme in conjunction with carbonate microfacies analysis. The ecologic range of each species should be determined with as much precision as possible to confirm whether the bimodal size trend is consistent. In addition, morphologic data bearing on growth rate would be useful. The larger individuals found at each extreme of the species range should grow at different rates.

Life History, Heterochrony, and Environmental Stress

The results of this investigation can be profitably interpreted using the concepts of heterochrony and environmental stress. Relative to most foraminifera, LBF have been considered "*K*-strategists" because of their protracted reproductive cycles, brooding of asexually-produced young,

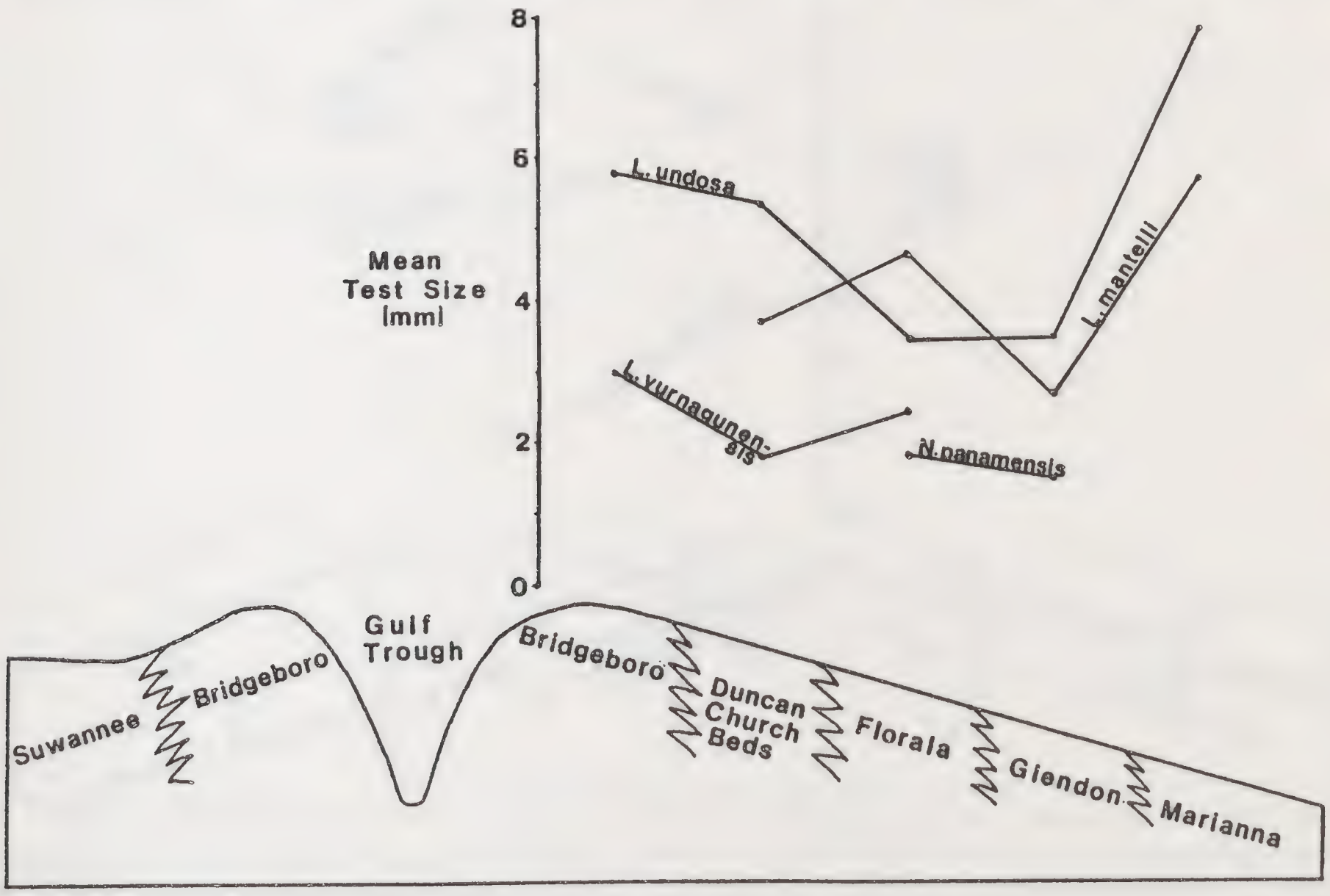


Figure 5. Species mean test size plotted against the facies in which it occurs.

slow growth, growth to large size, and occurrence in relatively stable environments (Hottinger, 1982, 1983). But at a finer scale of analysis, stress adaptation may also be evident.

Along the shallow, high energy/high illumination to deep, low energy/low illumination gradient, differences in growth rate and reproductive schedule should occur. At the shallow end, high light intensity and water energy facilitate relatively rapid growth. This environment and its resources, however, are not ephemeral, so there is no advantage to reproducing early (as would an *r*-strategist). Also, selection for either larger, or more, juveniles requires reproduction at large sizes. Growth is prolonged and reproduction delayed, but test calcification is efficient (producing robust, ornamented tests). Large size is thus reached by *hypermorphosis*. Such populations are *K*-selected relative to deeper populations.

In deeper waters, low light reduces the efficiency of algal symbiont photosynthesis and test calcification, and selection is for large juveniles that inherit much symbiont-rich protoplasm from the parent. Like the shallower populations, growth is prolonged, but at a slower rate. Large size is thus attained by hypermorphosis, but with a reduced rate of growth and perhaps less efficient calcification of the test. These populations are stress-selected.

As illustrated in Figure 10, these two developmental extremes represent end-members along a gradient of environmental *optimality* and *stress*. Environmental *disturbance* is not, strictly, a variable. Although a high energy coral reef might be considered a frequently disturbed environment, it is comparatively stable (seasonally) and does not fluctuate rapidly in food resources, temperature, salinity, etc. Therefore, life history strategies normally associated with *r*-selection are not found.

VI. CONCLUSIONS

For the symbiont-bearing larger foraminifera, primary stress factors are low light intensity and water energy. In oligotrophic, tropical to subtropical waters, light intensity and water energy are generally inversely related to water depth. The results of this study suggest that along a gradient of environmental stress and optimality (a depth gradient), intraspecific LBF body size and embryon size are pre-

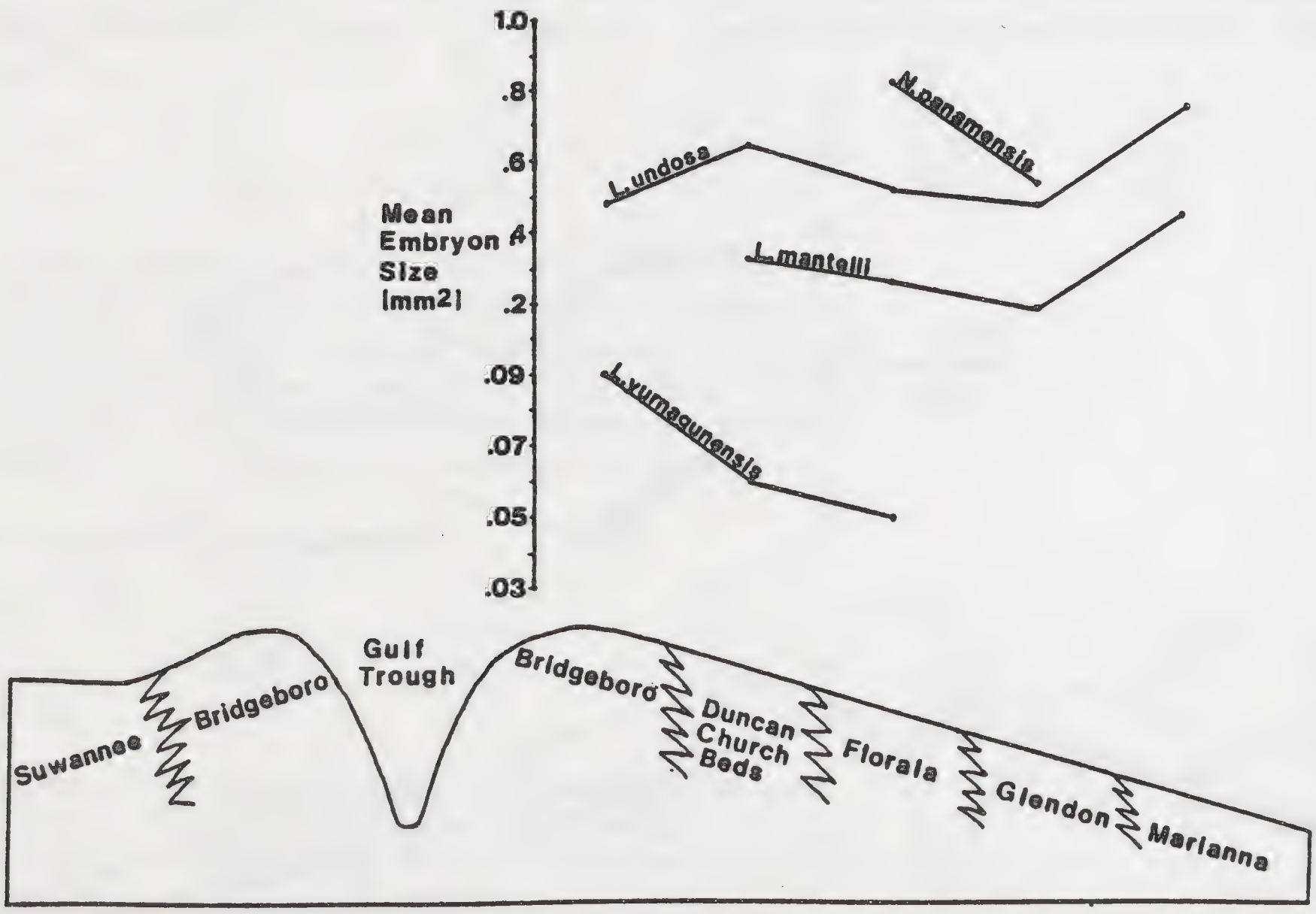


Figure 6. Species mean embryon size (area) plotted against the facies in which it occurs.

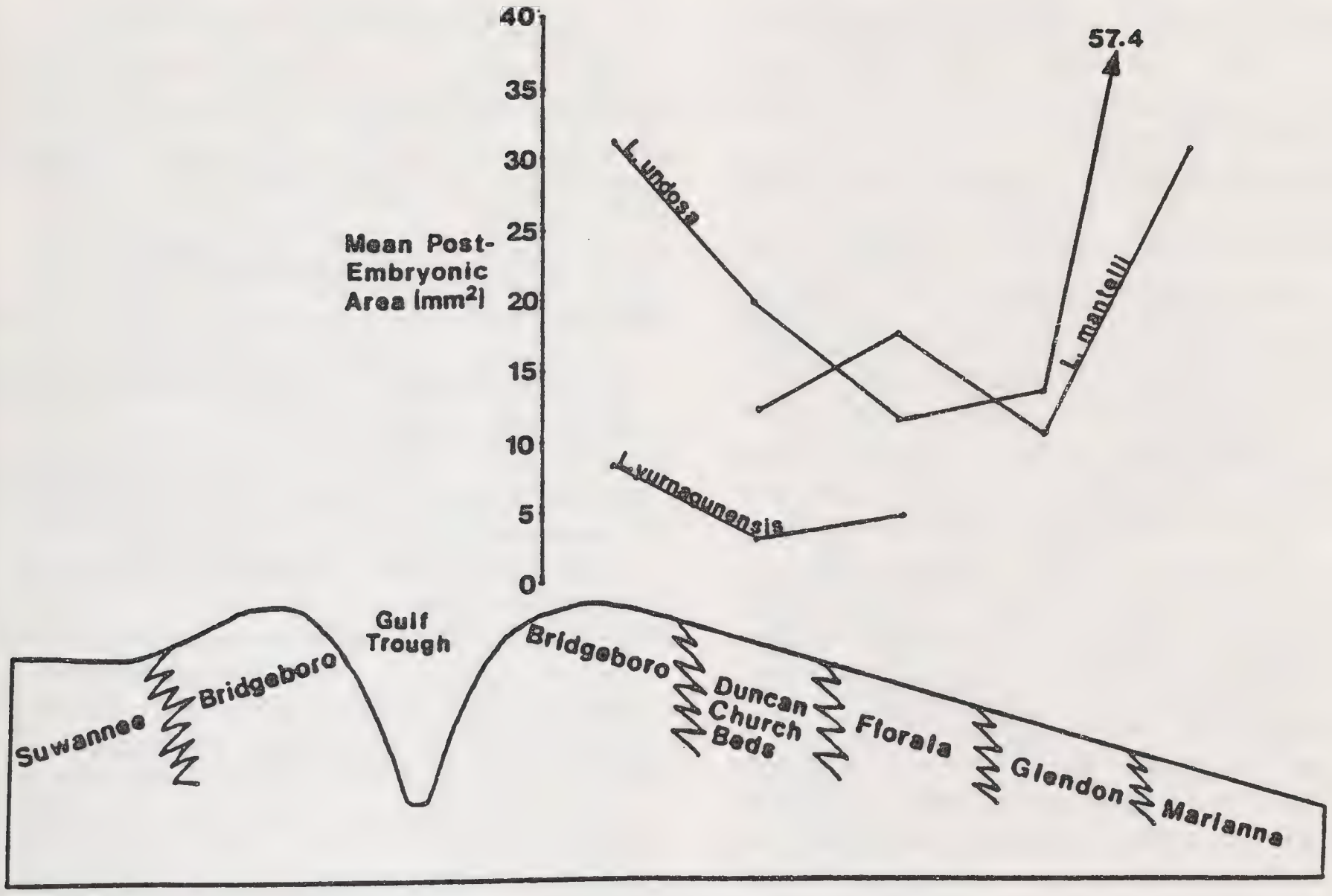


Figure 7. Species mean post-embryon size (area) plotted against the facies in which it occurs.

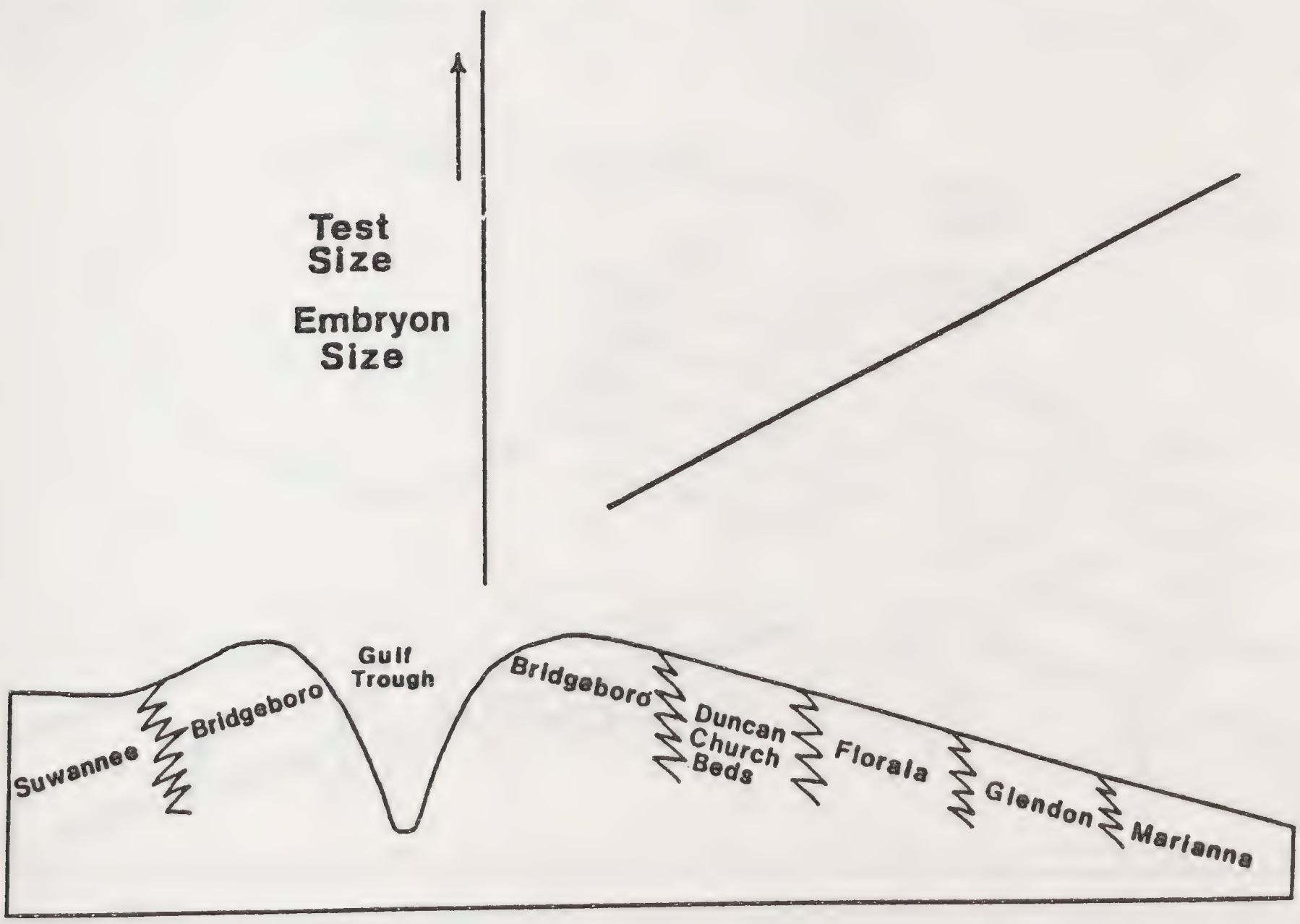


Figure 8. Diagramatic representation of the original hypothesis of this investigation. It was expected that both test size and embryon size would increase with depth along the paleoenvironmental gradient.

dicted to be greatest at the extremes of a species' range. At these limits, however, large size is attained by different means and for different reasons.

At the deep end of the ecogradient, LBF delay reproduction and grow more slowly (neotenic hypermorphosis). Large juveniles (with much symbiont-rich protoplasm) are favored under these low light conditions. These populations are under stress-selection. At the shallow end of the range, reproduction is also delayed (to increase either fecundity or juvenile size because of low juvenile survival in high energy conditions), but because of low stress, growth rate is normal or even slightly accelerated (hypermorphosis). These populations are under *K*-selection. Environmental variables, therefore, exert a direct influence on the life history and development of larger foraminifera. By delaying reproduction (hypermorphosis) to increase fecundity or juvenile size at the extremes of a species' range, larger intraspecific body sizes result.

VII. ACKNOWLEDGMENTS

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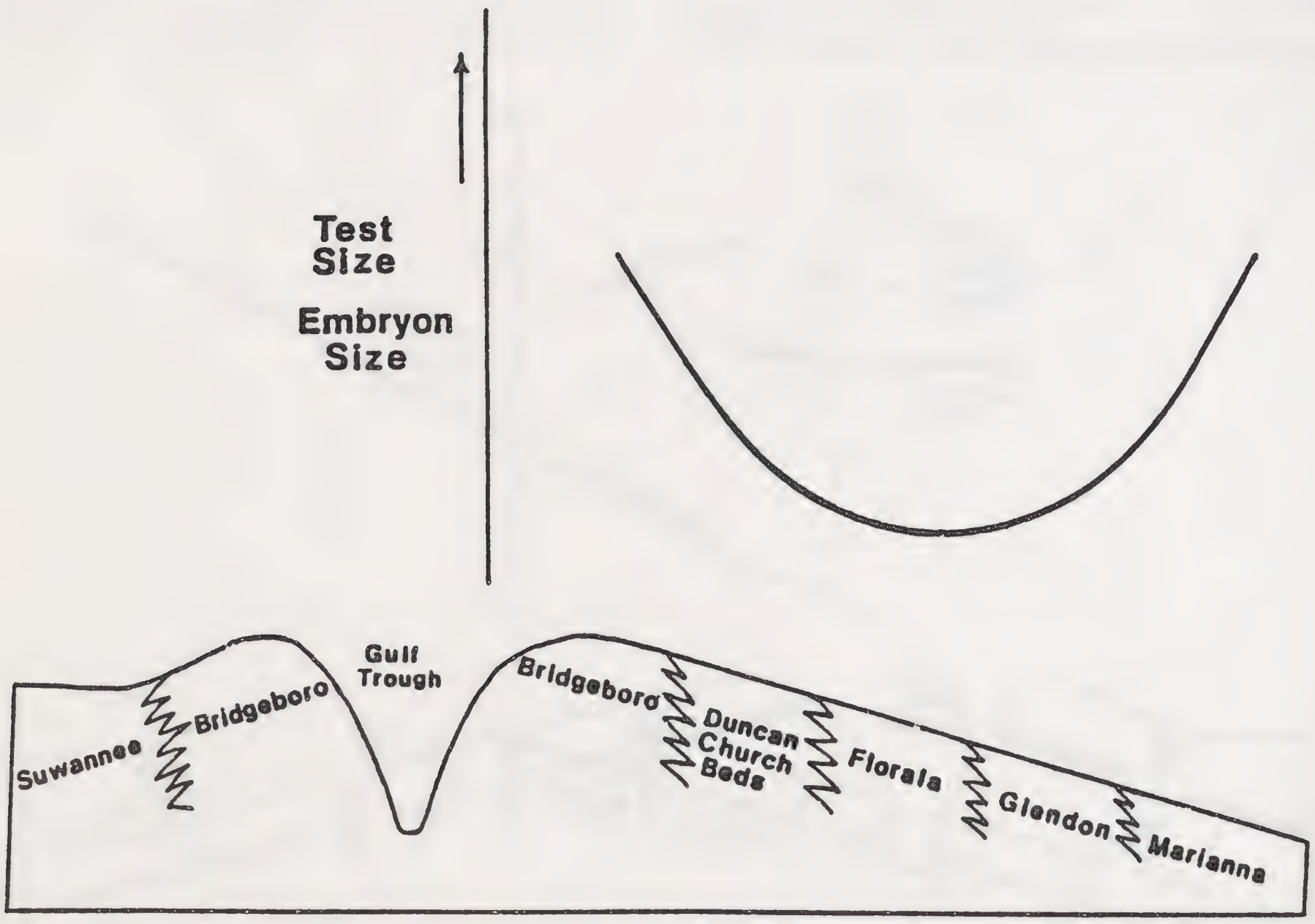

Figure 9. Diagramatic representation of the new, modified hypothesis generated by the data of this investigation. It is predicted that a species' test size and embryon size will increase at both extremes of its range along a shallow to deep paleoenvironmental ecogradient.

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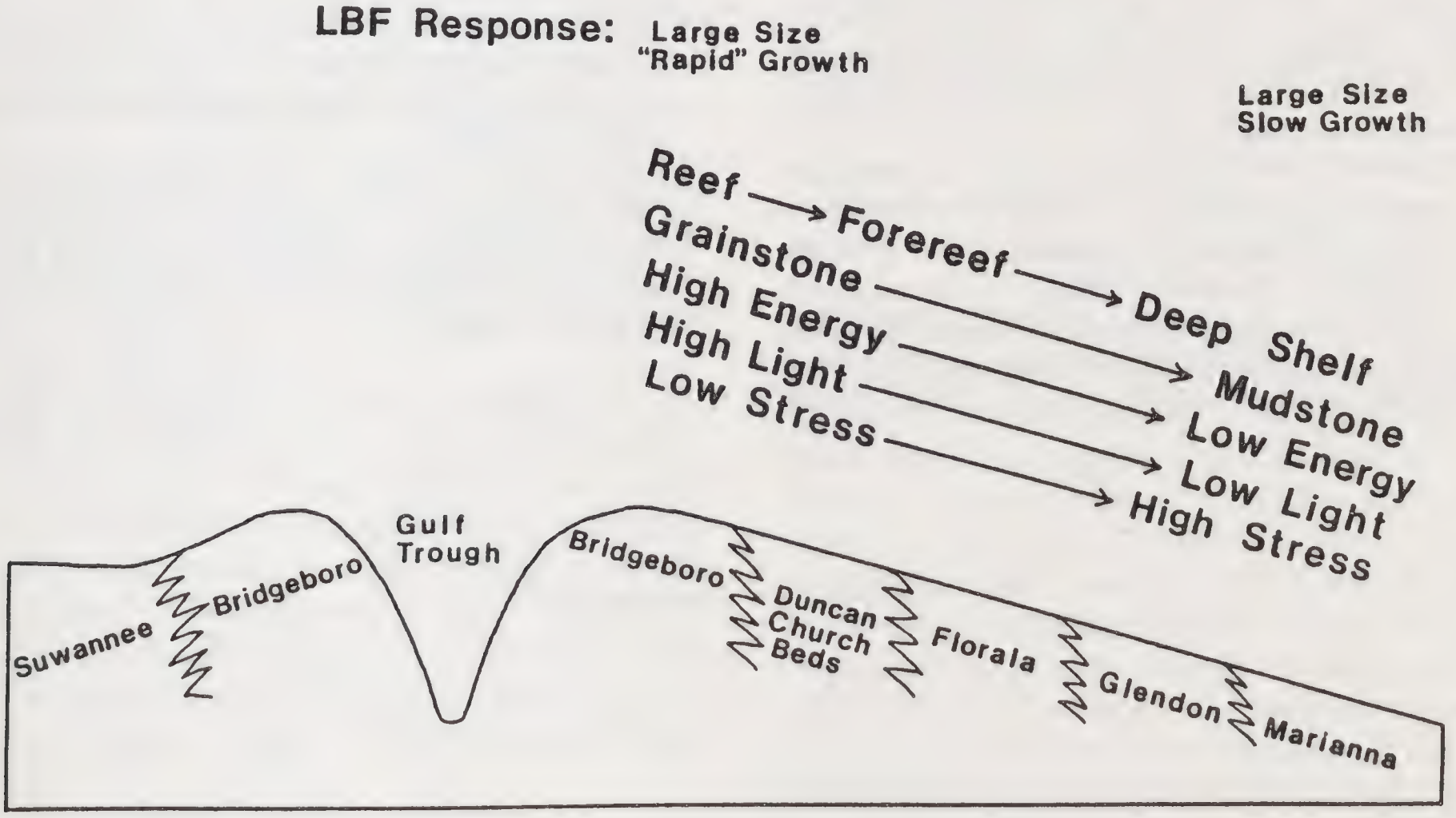

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NEW MOLLUSCAN FAUNAS FROM THE EOCENE OF SOUTH CAROLINA

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I. ABSTRACT

Over 80 Eocene molluscan species have been identified from the Southern Aggregates Orangeburg quarry near Cross, South Carolina, doubling the total reported fauna from the Santee Limestone. Use of latex peels and casts greatly facilitated the identification of leached aragonitic species. Some supposed endemics proved to be synonymous with Gulf Coast species. About 50% of the molluscan species collected at this quarry are also found in the Cook Mountain Formation and 35% are found in the Gosport Sand. The faunule from the nearby Martin Marietta Berkeley quarry is similar. The chronological ranges of some species found at these localities differ between South Carolina and the Gulf Coast. Some distinctive endemics are present, including a new genus, *Santeevoluta* (Volutidae), as well as taxa previously known solely from the Gulf Coast or Florida.

Younger deposits are present in the Giant Portland quarry, near Harleyville, South Carolina. Taxa include the new species *Batequeus ducenticostatus* (Pectinidae). Additional material from the Martin Marietta Georgetown and Southern Aggregates Jamestown quarries, near Jamestown, South Carolina, represents a deeper water facies of the Santee Limestone.

II. INTRODUCTION

Although the Eocene marine deposits in South Carolina have been known as long as those of the Gulf Coast, they have received much less study. This is partially because of nature of the deposits. Today the type locality of the Santee Limestone at Vance's Ferry is mostly under Lake Marion (Cooke and MacNeil, 1952). Current exposures are primarily in limestone quarries and, because of mining operations, accessibility is relatively ephemeral. Erosion, diagenesis, and poor preservation all have discouraged stratigraphic work in the Atlantic Coastal Plain (Owens, 1992).

The planktic foraminifera and nannofossils of the Eocene limestones of the Carolinas remain poorly known in comparison to those of the Gulf Coastal Plain. Foraminiferal and nannofossil correlations between these regions are currently inadequate and, in some instances, even contradictory (Laws, 1992). Likewise, molluscan biostratigraphic data for the Eocene limestones of the Carolinas, Georgia, and Florida remain sparse and are commonly limited to tentative identifications. In most cases, the synchronicity between ranges of potential index species in the Gulf and Atlantic Coastal Plains remains untested. Planktic microfossils are more accurate biostratigraphic markers than are the molluscs, being uninfluenced by substrate differences and less prone to regional diachronisms. However, microfossils tend to be poorly preserved in samples from the quarries, and cores are often difficult to correlate with quarry outcrops. Thus, macrofossils must be used for biostratigraphy of these beds until microfossil and macrofossil occurrences are better correlated.

The present study aims to provide more accurate and more complete taxonomic information on the molluscan faunas of the Eocene Santee and "Cross" formations of South Carolina in order to build a foundation for future, more detailed biostratigraphic comparisons. Preliminary assessments of biostratigraphic significance are offered for certain taxa and for molluscan faunas as a whole. Although limited by time averaging and incomplete knowledge of both species composition and biofacies controls, the present faunal comparisons provide a tentative basis for regional temporal correlation.

III. PREVIOUS WORK

Various workers have examined South Carolina Eocene faunas since their discovery about 1830. Lyell (1845) generally is considered the first to have recognized the Eocene age of the "white limestone of South Carolina." Conrad (1848a, 1848b) briefly described several mollusks from the collections of a Mr. Vanuxem from the "Orangeburg District," and this region has remained important for the Eocene of South Carolina. Tuomey (1848) and Sloan (1908) discussed these strata in their works on South Carolina geology. Harris *in* Van Winkle and Harris (1919) described some Eocene bivalves from the Santee Limestone. Cooke (1936) provided brief species lists for several Eocene localities in South Carolina, and Harbison (1944) reported 20 molluscan species from the Santee Limestone.

Cooke and MacNeil (1952) redefined the McBean Formation and Santee Limestone, restricting them to the *Cubitostrea sellaeformis* range zone (not a permissible method of defining lithostratigraphic units by current stratigraphic rules), redefined the Castle Hayne Limestone as a Gosport Sand equivalent, and applied the names Santee and Castle Hayne to beds in both North and South Carolina. Unlike Cooke and MacNeil, Pooser (1965) used lithologic definitions for the Eocene formations of South Carolina, in accord with modern stratigraphic rules. Palmer and Brann (1965-1966) noted 45 molluscan species recorded from the Santee Limestone.

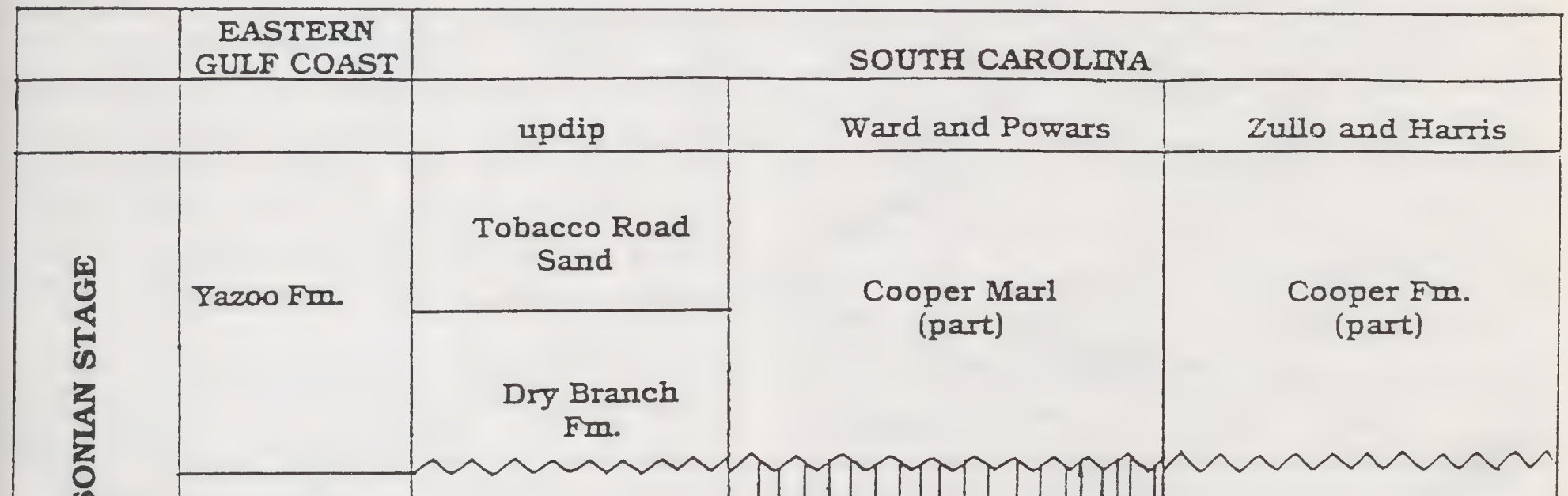
Banks (1977) recognized several lithozones in the Santee Limestone and suggested that lower Lisbon Formation and Gosport Sand equivalent beds were present, but did not name them. A flurry of papers from 1978 to 1982 named several members and formations in the Middle Eocene to Lower Miocene of North and South Carolina (Baum, Harris, and Zullo, 1978, 1979a; Ward, Lawrence, and Blackwelder, 1978; Ward *et al.*, 1979; Baum *et al.*, 1979, 1980; Baum, 1980, 1981; Ward and Blackwelder, 1980; Powell and Baum, 1982). Although faunal lists are often supplied in these papers, they were intended for stratigraphic rather than taxonomic purposes. In the South Carolina Eocene, all of these papers use the name "Santee Limestone" for the hard, moldic Middle Eocene limestone in South Carolina. The softer, younger limestone in South Carolina, called "Castle Hayne" by Cooke and MacNeil (1952), is referred to as the Cross Member of the Santee Limestone or the Cross Formation, but this designation is not stratigraphically valid. The stratotype of the Cross Member is actually lithologically similar to the typical Santee Limestone (L.W. Ward, pers. comm.). Text-figure 1 summarizes current views of the Eocene stratigraphy of the limestones of South Carolina.

Although current workers seem to agree that the contact between the Santee Limestone and the "Cross Formation" is chronologically equivalent to the upper Lisbon Formation-Gosport Sand contact in Alabama, no consensus exists on the age of the basal Santee or youngest "Cross." Also, the confusion over definitions of stratigraphic units makes it difficult to determine how a given sample fits into any particular stratigraphic scheme. For example, because there are two slightly different uses of the name "Cross," one must establish the actual beds sampled before faunal lists from the "Cross Formation" can be interpreted. Most stratigraphic units in the region were defined in outcrop, whereas microfossils are often better preserved in cores, which must be correlated to the stratotypes. Thus, any stratigraphic chart of the Eocene of South Carolina must presently be considered tentative.

One particular difficulty in correlating these faunas has been the diachronous appearance of traditional index taxa in South Carolina and the Gulf. Dockery and Nystrom (1992a), in a study of the molluscan

faunas of the upper Coastal Plain of South Carolina, noted the presence of Gosport Sand index species such as *Glyptoactis alticostata* and *Crassatella alta* in the Santee Limestone, along with the Cook Mountain Formation and upper Lisbon Formation index species *Cubitostrea sellaeformis*. They suggested that the warm current flowing through the Gulf Trough would have been an effective barrier to dispersal between the warm carbonate province of the southeastern states and the turbid clastic province of the Gulf Coast. Thus, *Glyptoactis alticostata* and *Crassatella alta* seem to have evolved in the carbonate province in the late Claibornian and invaded the clastic province only in the latest Claibornian.

In contrast to the 50 or so species reported in the literature from the Santee Limestone, this study has found over 80 molluscan species at the Southern Aggregates Orangeburg quarry alone and over 120 molluscan species from the Santee Limestone (excluding the "Cross" Member or Formation). Approximately half of the molluscan species in my collections from the Eocene of South Carolina have not been previously reported from the state. Also, some taxa previously described from

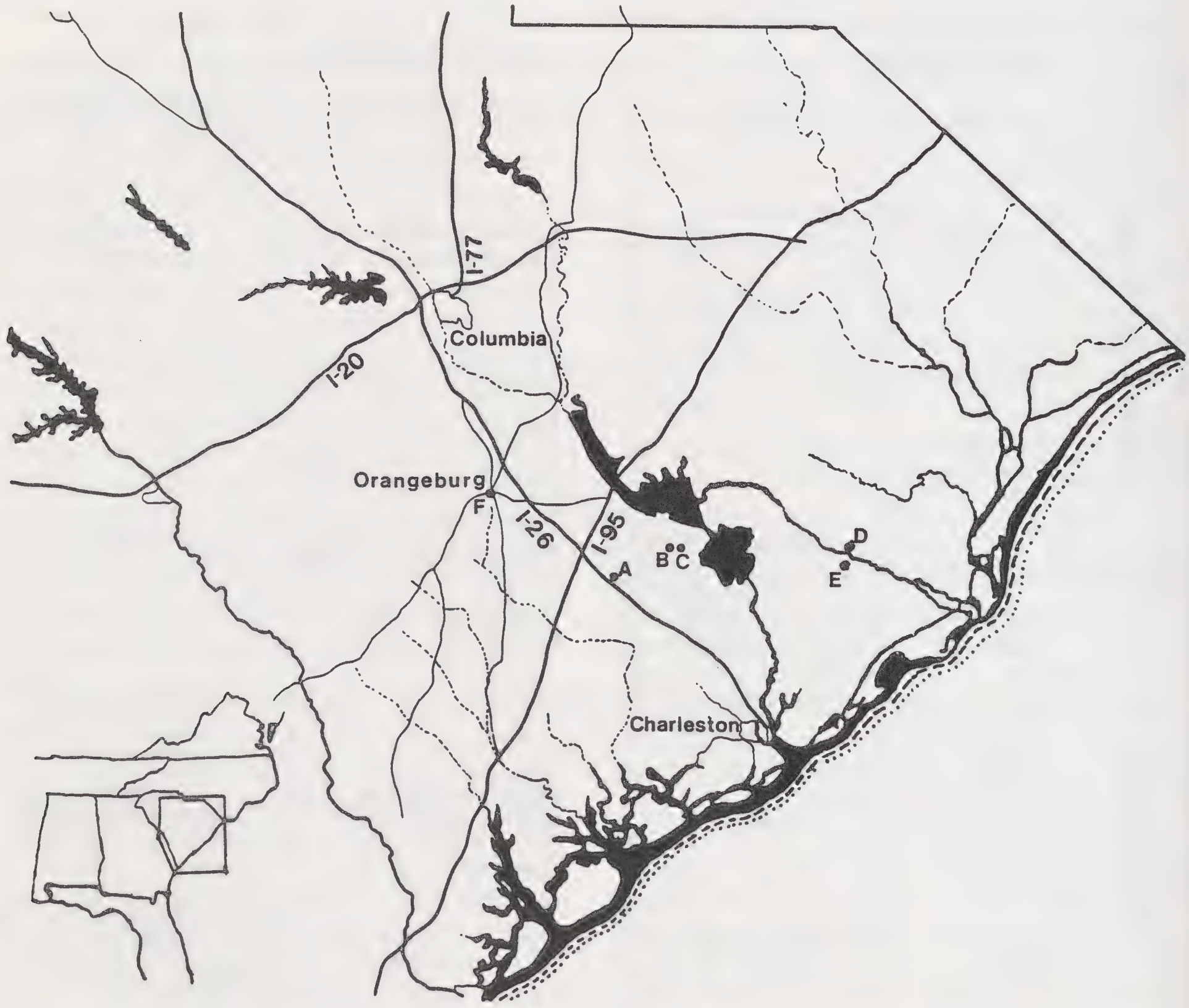


Text-figure 1. Eocene stratigraphy of South Carolina. Little consensus exists on nomenclature and correlation. Adapted from Zullo and Harris (1987, p. 197-214); Rossbach and Carter (1989, correlation chart); Ward and Powars (1991, p. 161-201); and Fallaw and Price (1992, p. B-II-1 – B-II-33). The quotation marks around "McBean" reflect doubts, raised by Fallaw and Price, about the use of this name. Also, the use of the name "Cross" is in doubt as the stratotype is part of the Santee Limestone (see text).

molds are junior synonyms, mostly of Gulf Coast species. Both the Santee and "Cross" faunas include undescribed species.

IV. LOCALITIES STUDIED

Specimens examined in this study were collected at six localities in south-central South Carolina (Text-figure 2), in Dorchester, Orangeburg, Berkeley, and Georgetown counties. The "McBean Formation" and Orangeburg District bed are updip (*i.e.*, west and slightly north) of the Santee Limestone localities. Some comparison material was obtained from "McBean Formation" deposits, including both the silicified shell-bearing Orangeburg District bed and a lower moldic limestone to calcareous marl bed, at the Dockery and Nystrom (1990, 1992a) locality N-25. The "Cross Formation" specimens are from the Giant Portland cement quarry (GP) between Holly Hill and Harleyville in Dorchester County. Santee Limestone material was obtained from the Southern Aggregates Orangeburg quarry (SAO) and the Martin Marietta Berkeley quarry (MMB), near the town of Cross, S.C.; and the Martin Marietta Georgetown quarry (MMG) and



Text-figure 2. Localities represented in this study. The box on the inset indicates the area of the main map.

A = Giant Portland Quarry
B = Southern Aggregates Orangeburg Quarry
C = Martin Marietta Berkeley Quarry
D = Martin Marietta Georgetown Quarry
E = Southern Aggregates Jamestown Quarry
F = Dockery and Nystrom locality N-25

the Southern Aggregates Jamestown quarry (SAJ), near Jamestown, S.C. All four quarries are mined for crushed stone. Specimens from the quarries were, of necessity, collected only from boulders and spoil. However, the abundance of *Cubitostrea sellaeformis* in the boulders at SAO and MMB establishes their general location in section.

The Santee Limestone is indurated and very moldic, with common glauconite. It is typically gray but may be white, often with orange iron stains. Aragonitic shells are leached, leaving well-preserved molds, whereas calcitic shells are preserved. Molds are frequently hard to identify, but liquid latex can be used to make casts that are more readily identified. Also, a mold in a large boulder may not be feasibly extracted with a chisel, and so a latex cast may be the only practical method of collecting some specimens.

The "Cross Formation" limestone is less indurated than the Santee Limestone. It also contains abundant molds and calcitic or phosphatic fossils. Unlike the Santee Limestone, it is consistently creamy white. With weathering, boulders often develop a thin, black coating. Probably because of its poor induration, the "Cross Formation" has fewer well-preserved molds than the Santee.

V. RESULTS

Due to wide variations in species diversity at each locality, percent overlap (# of species in common/# of species at the locality, essentially Simpson's Index 2 [Frederiksen, 1980]) was used to determine the best correlation. Table 1 shows the correlations for the primary localities in this study and for the Santee Limestone as a whole. Other faunas that show at least a 20% overlap with one or more of the studied South Carolina Eocene assemblages are included.

The well-collected molluscan faunas from the *Cubitostrea sellaeformis* zone of the Santee Limestone correlated best to faunas from the upper Claibornian Cook Mountain Formation. For SAO, the overlap with the Cook Mountain Formation fauna (50%) is greater than the overlap with published faunas from the Santee Limestone (maximum 27%), reflecting the poor knowledge of South Carolina faunas. The affinities of the MMB fauna are similar to those of the SAO fauna. [Much of the Gulf Coast range data come from Palmer and Brann (1965-1966). As the name "Lisbon Formation" is preoccupied, they referred records from the upper Lisbon Formation of Alabama to the Cook Mountain Formation. Therefore, the Cook Mountain and upper Lisbon formations are together in the table.]

TABLE 1
MAJOR CORRELATIONS–PERCENT OVERLAP

Locality	SAO	MMB	all Santee
SAO	100.0	95.8	98.4
MMB	38.3	100.0	39.3
Gosport Sand	40.0	33.3	39.3
Cook Mt., upper Lisbon Fms.	53.3	62.5	54.1
Castle Hayne Ls.	38.3	66.7	37.7
Orangeburg District bed	41.7	29.2	41.0
number of species	60	24	61

These figures do not include undescrbed species or taxa not yet identified to species.

All Santee = all Santee Limestone, *Cubitostrea sellaeformis* zone records from this study.

Gosport Sand, Cook Mountain Formation, and upper Lisbon Formation records from Palmer and Brann (1965, 1966) and Dockery (1980). Orangeburg District bed records from Dockery and Nystrom (1990, 1992a) and the present collections. Castle Hayne Limestone records from the present collections.

The faunas from MMG, SAJ, and GP are not adequately documented to draw firm conclusions about their overall affinities. Most species identified from MMG and SAJ are also known from SAO and MMB. However, patterns of abundance are different, with many rare or absent at the more inland localities (SAO and MMB) but common at MMG and SAJ. These species tend to be common in the Castle Hayne Limestone near Wilmington, N.C., equally distant from Eocene nearshore deposits. Probably, these species favored deeper water environments. The GP fauna seems distinct from the other South Carolina faunas. It correlates best with faunas from the lower Jacksonian Moodys Branch Formation (9 taxa identified to species, 4 also in Moodys Branch, 2 also in Gosport), but the low number of species limit the reliability of these conclusions.

The faunas of the Santee Limestone and the "Cross Formation" appear strongly influenced by the warm current flowing through the Gulf Trough (Popenoe *et al.*, 1987). In addition to producing a temperature gradient, the current would have provided a route of invasion for Tethyan taxa. The offshore carbonate environment of the Carolinas formed a distinct province from the Gulf Coast in the Eocene (B. Carter, 1987), though the clastic province of the inner Coastal Plain of South Carolina may have provided a bridge for Gulf Coast species to reach the carbonate province and vice versa.

VI. ACKNOWLEDGMENTS

I thank Wallace Fallaw for introducing me to the Eocene of South Carolina. The owners and operators of all the quarries were helpful in allowing me to collect at the various localities. David Dockery, Jerry Howe, Andrew Howard, Joseph Carter, Warren Blow, Elana Benamy, Gary Rosenberg, and Roger Portell provided access to collections. Many people have edited drafts of this paper, including David Grant, William Lammers, Victor Zullo, Lyle Campbell, Joseph Carter, David Dockery, Thomas Yancey, and Warren Allmon. David Dockery and Paul Nystrom provided information on and directions to the Orangeburg locality (N-25). Many of these individuals have also provided assistance in identification of various taxa. Joseph Carter, Thomas Rossbach, and Rebeccah Grey assisted with photography. Funds have been provided by the Southeastern Section of the Geological Society of America, the Undergraduate Science Research Program of the Merck Company Foundation, a National Science Foundation Fellowship, a Geological Society of America Research Grant, and a Martin Research Fellowship. Finally, I wish to thank my family, whose efforts in collecting, photography, editing, encouraging, and all other aspects made this study possible.

VII. SYSTEMATIC PALEONTOLOGY OF SELECTED TAXA

Over 350 species of mollusks are known from the Eocene of South Carolina, either from literature records or from my collections. Among these, this paper discusses several species that are inadequately described in literature. These include species with regional synonyms, frequently misidentified species, and forms with wider geographic or chronological ranges than previously thought. The synonymies include the original descriptions as well as references not found in Palmer and Brann (1965-1966).

A question mark in front of a species name indicates uncertainty in synonymizing the name with the species under discussion, whereas a question mark by an author's name indicates uncertainty of the validity of the record (usually species reported without figures or description). Personal observation of some collections has allowed me to assess some records such as the Sloan collections at the USNM, described by Vaughan (*in* Veatch and Stephenson, 1911); the Cooke collections at the USNM, cited in Cooke (1936) and Cooke and MacNeil (1952); the Santee-Cooper Canal collection of Richards at the ANSP described in Harbison (1944); and the Dockery and Nystrom Orangeburg area collections (cited in Dockery and Nystrom, 1990, 1992a, 1992b). Some of the Banks and Powell field collections are at the University of North Carolina-Chapel Hill. These were part of the material used to make the species lists in such works as Banks (1977), Baum (1980), Baum *et al.* (1980), Howe (1987), and Powell and Baum (1982); however, they did not indicate

which specimen was the basis for which published record.

Phylum MOLLUSCA
Class BIVALVIA
Subclass PTERIOMORPHIA
Order PECTINOIDA
Superfamily PECTINOIDEA
Family PECTINIDAE
Genus CHLAMYS Röding, 1798

CHLAMYS (AEQUIPECTEN?) CACAWENSIS
(Harris)
Plate 1, figure 1

Pecten cawcawensis HARRIS, 1919, Bulls. Amer. Paleontology, v. 6, p. 27, pl. 15, figs. 1-7.

Pecten (Chlamys) membranosus Morton. HARBISON, 1944, Acad. Nat. Sci. Phila., Not. Nat., no. 143, p. 3, pl. 1, fig. 5 [not *P. membranosus* Morton, 1833].

Chlamys cawcawensis (Harris). PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 81; TOULMIN, 1977, Geol. Survey Alabama, Monograph 13, p. 313, 354 [in part, not Jackson records]; ZULLO and HARRIS, 1987, Cushman Found. Foram. Research, Spec. Publ. 24, p. 207; DOCKERY and NYSTROM, 1990, Proc. Second Bald Head Island Conf. (conference version), p. 86; DOCKERY and NYSTROM, 1992a, *ibid.* (revised version), p. 95.

Not *Chlamys cawcawensis* (Harris). GLAWE, 1974, Georgia Geol. Survey Inform. Circ. 46, p. 8; TOULMIN, 1977, Geol. Survey Alabama, Monograph 13, p. 313, 354 [in part, Moodys Branch records], pl. 54, figs. 12, 13; BAUM, HARRIS, and ZULLO, 1979, *in* G.R. BAUM, W.B. HARRIS, and V.A. ZULLO (eds.), Structural and Stratigraphic Framework for the Coastal Plain of North Carolina, p. 9; BAUM *et al.*, 1979, *ibid.*, p. 89, 91; BAUM *et al.*, 1980, South Carolina Geology, v. 24, no. 1, p. 23; POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1101, 1105. See *Chlamys (Aequipecten)* n. sp.

Not *Chlamys* aff. *C. cawcawensis* (Harris). BAUM, HARRIS, and ZULLO, 1978, Southeastern Geol., v. 20, no. 1, p. 11; BAUM, HARRIS, and ZULLO, 1979, *in* G.R. BAUM, W.B. HARRIS, and V.A. ZULLO (eds.), Structural and Stratigraphic Framework for the Coastal Plain of North Carolina, p. 9; BAUM, HARRIS, and ZULLO, 1979, *ibid.*, p. 101; BAUM, 1981, Southeastern Geol., v. 22, no. 4, p. 181. See *Chlamys (Aequipecten)* n. sp.

Discussion: Baum *et al.* (1979, p. 89) listed *Chlamys cawcawensis* among "the faunal elements which have generated the greatest confusion" in the Eocene of the Carolinas. Harris (1919) obtained the syntypes of *C. cawcawensis* from the "McBean Formation" (probably not the silicified Orangeburg District Beds of Dockery and Nystrom, 1992a). However, these specimens are poorly preserved. Harris also figured a complete specimen from Alabama (1919, pl. 13, fig. 8) and suggested that it might be a variety of *C. cawcawensis*. Many later authors have used this specimen in their species concept (*e.g.*, Toulmin, 1977, whose specimens from the Moodys Branch Formation closely resemble this one). The Alabama specimen is not conspecific with the syntypes, having smooth, uniform primary ribs, whereas true *C. cawcawensis* has fine concentric sculpture on the primary ribs, which bifurcate irregularly.

The name has been widely misapplied to a younger species common at GP, as discussed below. Both species have narrow interspaces, although those of true *Chlamys cawcawensis* are wider than those of the undescribed species. My specimens of this taxon are from SAO, MMB, and a locality with silicified shell north of Orangeburg, S.C.

CHLAMYS (AEQUIPECTEN) sp.
Plate 1, figure 2

Chlamys n. sp. ZULLO and HARRIS, 1986, *in* D.A. TEXTORIS (ed.), SEPM Field Guidebook, Southeastern United States, p. 258, 261, 263, fig. 5G.

Chlamys (Aequipecten) n. sp. ZULLO and HARRIS, 1987, Cushman Found. Foram. Research, Spec. Publ. 24, p. 207, 209, 210.

Chlamys n. sp. aff. *C. deshayesii* (Lea). COOKE and MACNEIL, 1952, U.S. Geol. Survey, Prof. Paper 243-B, p. 26; POOSER, 1965, Univ. Kansas Paleont. Cont., Arthropoda, art. 8, p. 18.

Chlamys cawcawensis (Harris). BAUM, HARRIS, and ZULLO, 1979, *in* G.R. BAUM, W.B. HARRIS, and V.A. ZULLO (eds.), Structural and Stratigraphic Framework for the Coastal Plain of North Carolina, p. 9; BAUM *et al.*, 1979, *ibid.*, p. 89, 91; BAUM *et al.*, 1980, South Carolina Geology, v. 24, no. 1, p. 23; POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1101, 1105.

Chlamys aff. *C. cawcawensis* (Harris). BAUM, HARRIS, and ZULLO, 1978, Southeastern Geol., v. 20, no. 1, p. 11; BAUM, HARRIS, and ZULLO, 1979, *in* G.R. BAUM, W.B. HARRIS, and V.A. ZULLO (eds.), Structural and Stratigraphic Framework for the Coastal Plain of North Carolina, p. 9; BAUM,

HARRIS, and ZULLO, 1979, *ibid.*, p. 101; BAUM, 1981, Southeastern Geol., v. 22, no. 4, p. 181.

Discussion: The "*Chlamys cawcawensis*" of the "Cross Formation" and upper Castle Hayne Limestone (New Bern or Spring Garden) is an unnamed species with wide, low, arched, regular ribs unlike the uneven, elevated, flat, bifurcating ribs of Harris's species (Zullo and Harris, 1987). The new species is moderately common at GP and is also present at various localities in North Carolina. It lacks the intercostal riblets of true *C. cawcawensis* and of the Gulf Coast taxon of Harris (1919, pl. 13, fig. 8) and Toulmin (1977, pl. 54, figs. 12, 13).

Powell and Baum (1982) cited *Chlamys cawcawensis* as an index fossil that indicates a Jacksonian age for the "Cross Formation." Baum, Harris, and Zullo (1978) recognized that the Jacksonian species were not *C. cawcawensis*, and referred to the species from the upper Castle Hayne as *Chlamys* aff. *C. cawcawensis*, but many subsequent publications missed the "aff."

CHLAMYS WAHTUBBEANA Dall
Plate 1, figures 3-7

Pecten (Chlamys) wahtubbeana DALL, 1898, Trans. Wagner Free Inst. Sci. Phila., v. 3, pt. 4, p. 736, pl. 34, fig. 9.

Pecten wahtubbeanus Dall. ?VAUGHAN *in* VEATCH and STEPHENSON, 1911, Georgia Geol. Soc., Bull. 26, p. 240 (very small juvenile).

Chlamys wautubbeana Dall. ?COOKE and MACNEIL, 1952, U.S. Geol. Survey, Prof. Paper 243-B, p. 24; ?POOSER, 1965, Univ. Kansas Paleont. Cont., Arthropoda, art. 8, p. 18; ?POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1100.

Chlamys wahtubbeana Dall. PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 88; TOULMIN, 1969, Trans. Gulf Coast Assoc. Geol. Soc., v. 19, p. 472; TOULMIN, 1977, Geol. Survey Alabama, Monograph 13, p. 245, 354, pl. 33, figs. 17, 18; DOCKERY, 1980, Mississippi Dept. Nat. Res., Bull. 122, p. 155, pl. 47, figs. 1, 2, 5; ZULLO and HARRIS, 1987, Cushman Found. Foram. Research, Spec. Publ. 24, p. 207.

Chlamys wautubbeanna [*sic*] (Dall). POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1105.

Pecten (wahtubbeanus var. *?) Willcoxii* DALL, 1898, Trans. Wagner Free Inst. Sci. Phila., v. 3, pt. 4, p. 737, pl. 29, fig. 4.

Chlamys wahtubbeana willcoxi (Dall). PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 89.

Pecten biddleana KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 8, 11, 20, pl. 2, fig. 4; HARBISON, 1944, Acad. Nat. Sci. Phila., Not. Nat., no. 143, p. 3, pl. 1, fig. 5.

Chlamys biddleana (Kellum). PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 80.

?"*Pecten* sp. cf. *biddleana*?" Kellum. DUBAR *et al.*, 1980, *in* R.W. FREY (ed.), Excursions in Southeastern Geol., v. 1, p. 234; J. CARTER *et al.*, 1988, North Carolina Geol. Survey, Bull. 89, p. 26.

?*Chlamys membranosa* (Morton). WARD *et al.*, 1978, U.S. Geol. Survey, Bull. 1457-F, p. F9.

?*Pecten membranosus* Morton. RICHARDS, 1950, Amer. Philos. Soc., Trans., n. s., v. 40, pt. 1, p. 15, 18, fig. 63d (as *membrabosus* lapsus calami); WARD and BLACKWELDER, 1980, *in* R.W. FREY (ed.), Excursions in Southeastern Geol., v. 1, p. 202.

"*Pecten*" sp. WARD, 1985, U.S. Geol. Survey, Prof. Paper 1346, p. 49, pl. 6, fig. 3 [not figs. 1, 2].

Discussion: This species is especially common in the collections from MMB and SAO and previously has been reported from the Santee Limestone and "McBean Formation." The type locality is Wautub-

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PLATE 1

Measurements are greatest length (l), height (h), or diameter (d) of the specimen. Original dimensions of incomplete specimens were not reconstructed.

1. *Chlamys cawcawensis*, original shell, SAO; UNC 15231; 25.7 mm (h).
2. *Chlamys (Aequipecten)* sp. nov., original shell, GP; UNC 8458a; 39.2 mm (l).
3. *Chlamys wahtubbeana*, original shell, MMB; specimen lost; 23.3 mm (h).
4. *Chlamys wahtubbeana*, original shell, MMB; specimen lost; 22.7 mm (h).
5. *Chlamys wahtubbeana*, original shell, MMB; UNC 8350; 22.2 mm (w).
6. *Chlamys wahtubbeana*, original shell, MMB; UNC 8363; 27.1 mm (h).
7. *Chlamys wahtubbeana*, original shell, MMB; UNC 12267; 24.0 mm (h).
8. *Batequeus ducenticostatus*, paratype, original shell, GP; UNC 12248a; 38.7 mm (h).

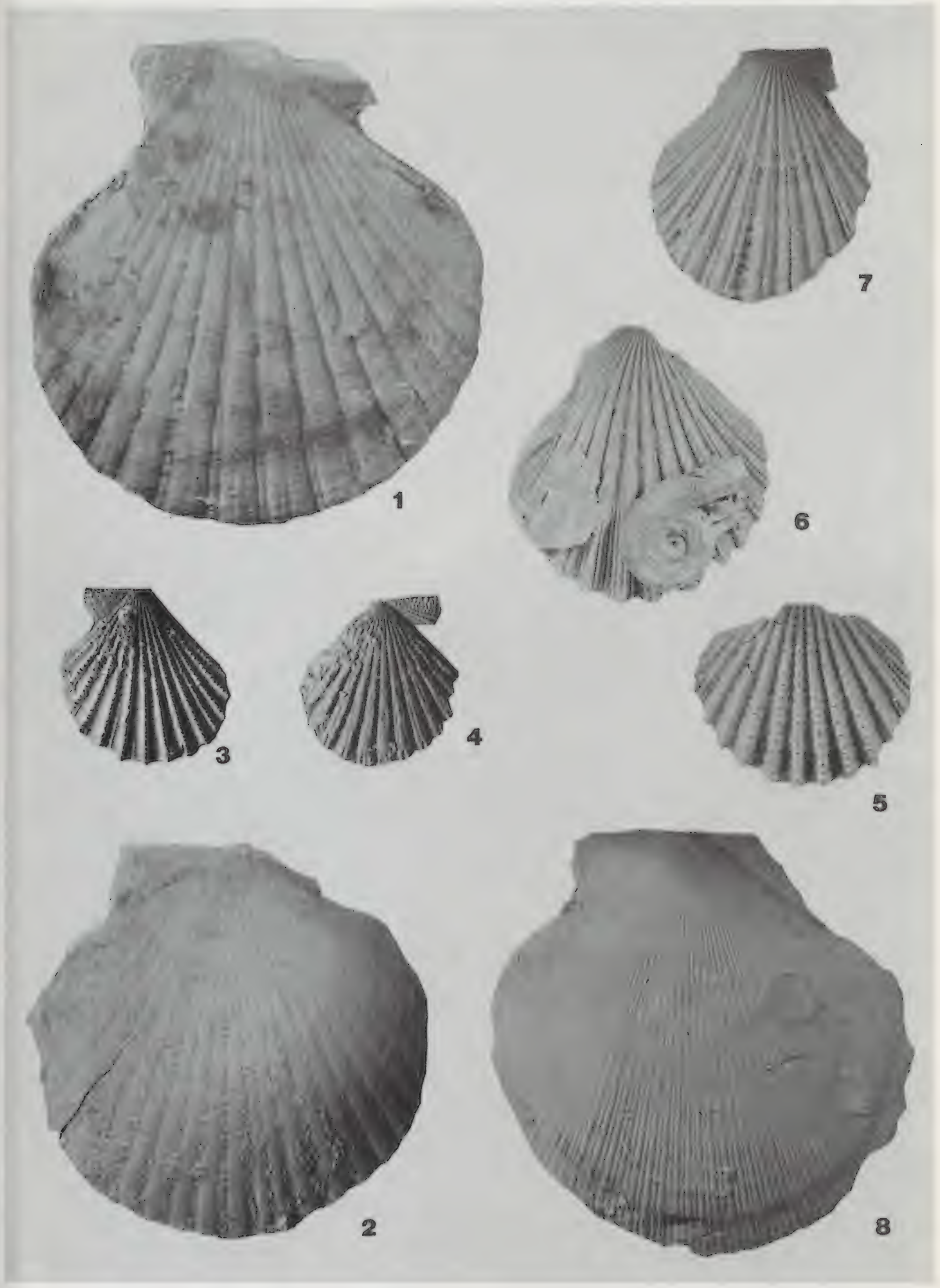

PLATE 1

bee, Mississippi, but the original spelling of the species was with an 'h' due to the "bad orthography of the collector" according to Harris (1919, p. 21). Harris (*ibid.*) observed that "this species is extremely variable in appearance, even at the type locality." Right and left valves commonly show different sculpture, and the pattern of sculpture on a single valve may show considerable ontogenetic change.

The range of variation includes *Chlamys wahtubbeana willcoxi* (Dall, 1898) and *Chlamys biddleana* (Kellum, 1926). The type of *C. biddleana* is eroded, making it appear somewhat different from well-preserved specimens. Frequently, the ribs of *C. wahtubbeana* develop a tricarinate form, with concentric sculpture ranging from fine prickles to overlapping laminae exaggerated to the exclusion of other sculpture. Other specimens have reduced the ribs to threads.

All specimens observed in this study have about 15 ribs and are somewhat longer than wide. Various authors have reported forms with more or fewer ribs: *e.g.*, variety "*tirmus*" as used by Harris (1919) and Rowland (1936); "*Pecten*" sp. of Ward (1985, pl. 5, fig. 1); *C. gilbertharrisi* Tucker (1931) (a junior homonym; renamed *C. beverlyi* Tucker, 1934). Judging by the lack of variation in rib number seen in *C. wahtubbeana*, these probably represent distinct species.

Ward *et al.* (1978) and Ward and Blackwelder (1980) synonymized *C. wahtubbeana* with *C. membranosa* (Morton, 1833). As recognized by Cooper (1981, cited in Zullo and Harris, 1987), the latter is a distinct taxon common in the Santee and Castle Hayne Limestones. The type lot of *Chlamys membranosa* (Morton) consists of about a dozen specimens. They are all smaller, more circular in outline, and more convex than *C. wahtubbeana*, with numerous (about 40) fine, thread-like ribs. No designation of a lectotype has been found, but none are conspecific with *C. wahtubbeana*. I cannot tell which forms Ward *et al.* (1978) intended to synonymize.

Genus BATEQUEUS
Squires and Demetrion, 1990
BATEQUEUS DUCENTICOSTATUS sp. nov.
Plate 1, figure 8; Plate 2, figures 1, 2; Plate 3, figures 1, 2

Chlamys n. sp. COOKE and MACNEIL, 1952, U.S. Geol. Survey, Prof. Paper 243-B, p. 26.

?*Chlamys cocoana* Dall. COOKE and MACNEIL, 1952, U.S. Geol. Survey, Prof. Paper 243-B, p. 26, 27; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 82.

?*Pecten cocoanus* Dall. WARD *et al.*, 1979, South Carolina Geol. Notes, v. 23, p. 23, 32; WARD and BLACKWELDER, 1980, *in* R.W. FREY (ed.), Excursions in Southeastern Geol., v. 1, p. 196; DUBAR *et al.*, 1980, *ibid.*, v. 1, p. 236.

?*Chlamys* cf. *C. cocoana* (Dall). POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1105.

Description: Adult shell produced posteriorly, adult height slightly less than length (maximum 55 mm), juvenile taller than long. Anterior auricle with fine radial sculpture, concentric growth lines prominent near byssal notch; byssal notch shallow; dorsal margin straight or slightly concave; posterior auricle with very faint, fine radial sculpture, narrow and smaller than anterior auricle. Shell thin. Left valve sculpture of about 25 primary radial ribs, which may bifurcate; first intercalary ribs (secondary ribs) appear at about 5 to 6 mm below beak and become equal to the primary ribs in size (about 0.5 mm wide at ventral margin in adult), later intercalary ribs (tertiary ribs) remaining narrower (0.3 mm at ventral margin); almost no interspace in well-preserved areas; fine scales not aligned from rib to rib. Right valve sculpture similar; about 30 primary ribs, with a greater trend towards bifurcation than in left valve; additional intercalary ribs possible, becoming equal in width to tertiary ribs, producing a pattern of three smaller ribs between each pair of large ribs in the center of the ventral edge. Sculpture of both valves finer towards anterior and posterior margins; easily eroded to form smooth, threadlike ribs with interspaces narrower than the ribs.

Holotype: USNM 466955.

Paratypes: USNM 466956; UNC 12248a.

Type locality: Giant Portland cement quarry, north of Harleyville, South Carolina. All known specimens of this species are from this locality.

PLATE 2

1. *Batequeus ducenticostatus*, paratype, original shell, GP; UNC 12248a; 11.3 mm (auricle length). Detail of anterior auricle from specimen of plate 1, figure 8.
2. *Batequeus ducenticostatus*, paratype, original shell, GP; UNC 12248a; 5.0 mm (photo width). Detail of sculpture from specimen of plate 1, figure 8.

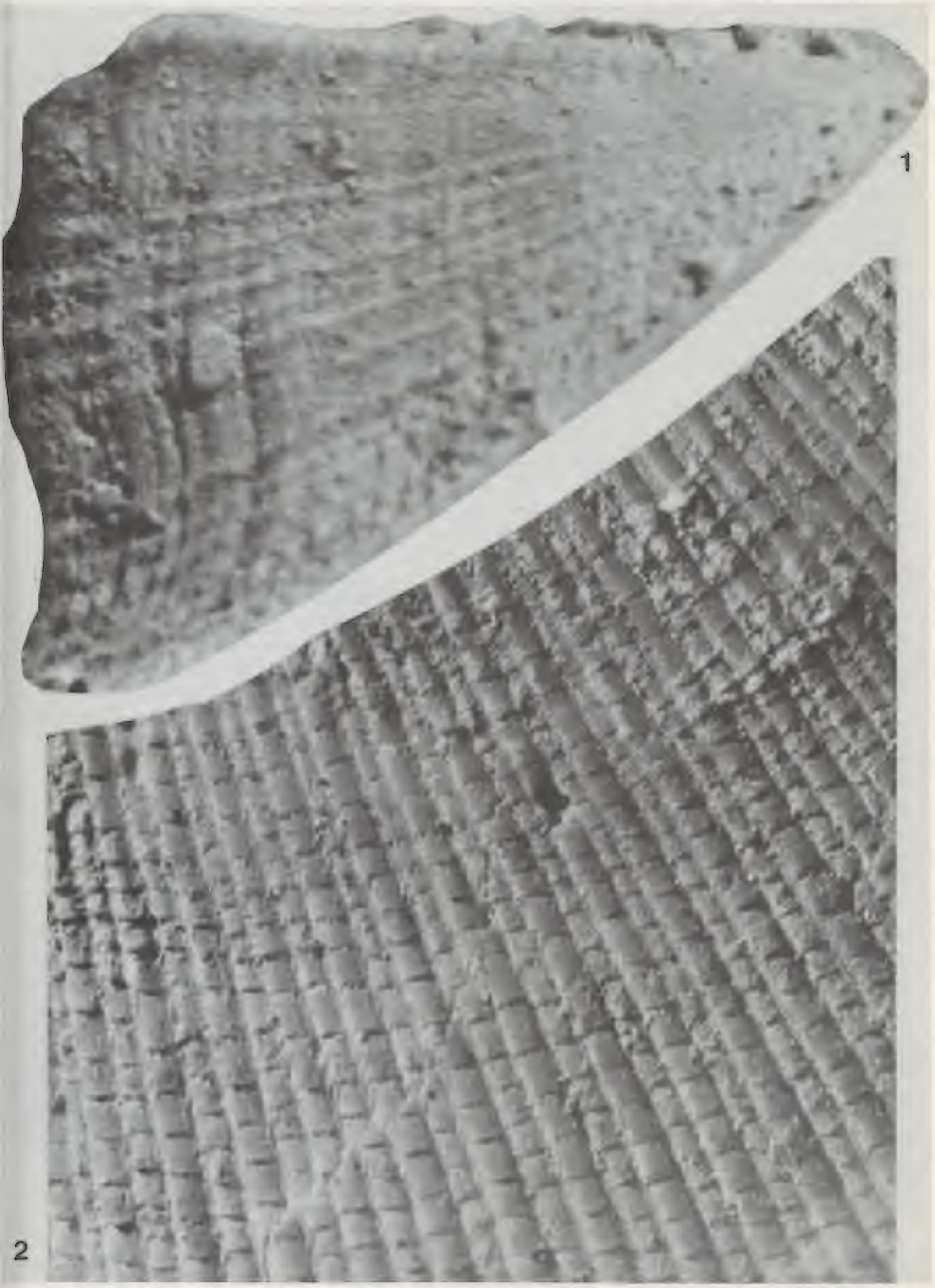

PLATE 2

Etymology: Adults have about 150 more ribs than any other Eocene scallop in the region; hence, "two hundred-ribbed" is a useful distinguishing feature.

Discussion: This species closely resembles *Batequeus mezquitalensis* Squires and Demetrion (1990), the type species of *Batequeus*. They are similar in size and shape, being slightly longer than high as adults. The valves in both species seem equally low-convex, but I do not have any articulated pairs of *B. ducenticostatus* for direct comparison. The byssal notch in both is small, but in *B. ducenticostatus* the anterior auricles are larger than the posterior ones, unlike *B. mezquitalensis*.

Both species have left valves with numerous very closely spaced riblets, though the scales are discontinuous and more widely spaced in *B. ducenticostatus*, as opposed to the "imbricated growth lines" of *B. mezquitalensis*. The right valve sculpture is more distinctive. Both have 25-30 primary ribs, but in *B. mezquitalensis* they are low, flat-topped, and can be grooved, unlike the fine, ungrooved, scaled riblets of *B. ducenticostatus*, which are similar to those of the left valve. Intercalary ribs are present on both valves of both species. In the largest specimens of *B. ducenticostatus*, three sets of intercalary ribs may be present, in addition to some bifurcation of primary ribs, producing a total of over 200 ribs ventrally. As noted by Squires and Demetrion (1990), *Batequeus* is assignable to the *Chlamys* group of Hertlein (1969). It seems closely related to the New Zealand genus *Serripecten*.

Batequeus ducenticostatus is distinct from all other known Eocene species from the eastern United States. The sculpture of the various forms in the type lot of *Chlamys membranosa* is finer but otherwise similar to that of *B. ducenticostatus*, but the latter attains a larger maximum size and differs greatly in shape. *Chlamys cocoana* (Dall, 1898) is similar in overall outline to *B. ducenticostatus*, but has wider, more irregular primary ribs and wider interspaces without the rapid development of intercalary ribs. Also, the type of *C. cocoana* is probably from the Oligocene (Cooke and MacNeil, 1952). Glawe (1974, pl. 2) figures what appear to be at least three species under this name, all of which have taller, wider primary ribs and less well-developed intercalary ribs than *B. ducenticostatus*. However, the form(s?) represented by his figures 1, 4, 7, and 8 are similar in shape of auricle and overall outline to *B. ducenticostatus*.

Records from the Cooper Formation of *Chlamys cocoana* (Ward *et al.*, 1979, p. 23; Ward and Blackwelder, 1980, p. 196; Cooke and MacNeil, 1952; Glawe, 1974) may represent true *C. cocoana* or *B. ducenticostatus* (in that case, the specimens probably were from the "Cross" and not the Cooper), or they may represent a new species.

Order OSTREOIDA
Superfamily PLICATULOIDEA
Family PLICATULIDAE
Genus PLICATULA Lamarck, 1801
PLICATULA FILAMENTOSA Conrad
Plate 3, figure 3

Plicatula filamentosa CONRAD, 1833, Fossil shells of the Tertiary formations of North America, v. 1, no. 3, p. 38; ?GARDNER *in* MILLER, 1912, North Carolina Geol. and Econ. Survey, Publ., v. 3, p. 188; KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 8, 11, 21, pl. 2, figs. 5, 6; ?RICHARDS, 1950, Amer. Philos. Soc., Trans., n. s., v. 40, pt. 1, p. 18; ?HARRIS, 1951, Bulls. Amer. Paleontology, v. 8, no. 138, p. 7, pl. 2, figs. 6-9; ?COOKE and MACNEIL, 1952, U.S. Geol. Survey, Prof. Paper 243-B, p. 24; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 280; TOULMIN, 1977, Geol. Survey Alabama, Monograph 13, p. 260, pl. 40, figs. 10-11; ?BAUM, HARRIS, and ZULLO, 1979, *in* G.R. BAUM, W.B. HARRIS, and V.A. ZULLO (eds.), Structural and Stratigraphic Framework for the Coastal Plain of North Carolina, p. 108; ?BAUM *et al.*, 1980,

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PLATE 3

1. *Batequeus ducenticostatus*, paratype, original shell, GP; UNC 12278b; 11.6 mm (photo width). Detail of right valve sculpture from the largest available specimen.
2. *Batequeus ducenticostatus*, holotype, original shell, GP; USNM 466955; 47.8 mm (l).
3. *Plicatula filamentosa*, latex cast, SAO; UNC 15444; 21.8 mm (h).
4. *Glyptoactis (Claibornicardia) alticostata*, latex cast, SAO; UNC 15449; 56.9 mm (l).

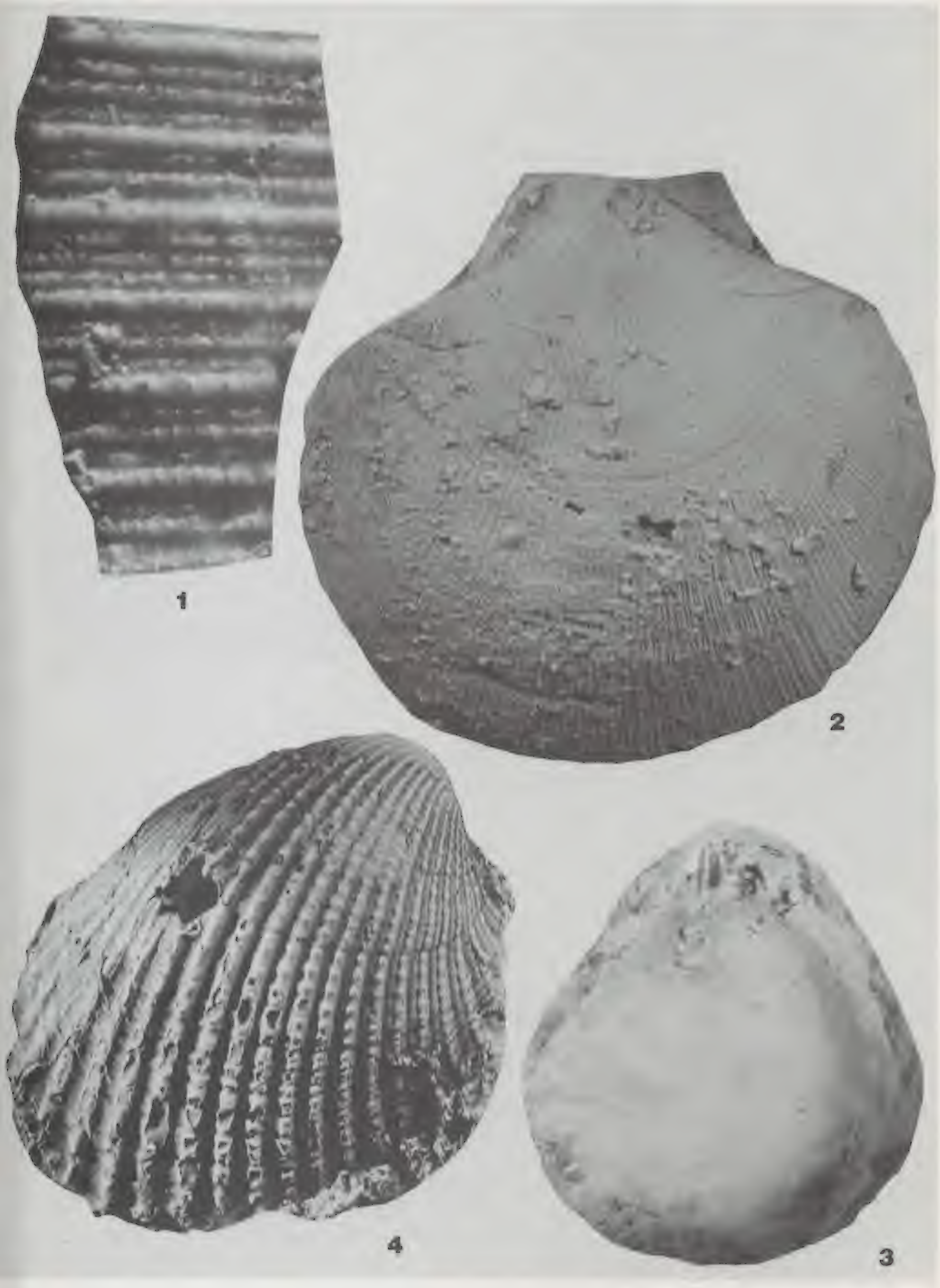

PLATE 3

South Carolina Geology, v. 24, no. 1, p. 26; ?BAUM, 1980, Southeastern Geol., v. 21, no. 3, p. 195; DOCKERY, 1980, Mississippi Dept. Nat. Res., Bull. 122, p. 159, pl. 47, fig. 7 [as var.?]; ?POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1105; WARD, 1985, U.S. Geol. Survey, Prof. Paper 1346, p. 49, pl. 5, fig. 7.

Plicatula filementosa [*sic*] Conrad. RICHARDS, 1955b, Georgia Mineral Newsletter, v. 8, no. 4, p. 152, first pl., figs. 2, 3.

Plicatula spp. PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 281, 282 [in part?].

Plicatula gibbosa Lamarck. ?HOWE, 1987, Rocks and Minerals, July/August, p. 241 [not *P. gibbosa* Lamarck, 1801 (Recent)].

?*Plicatula* sp. aff. *P. filamentosa* Conrad. SQUIRES and DEMETRION, 1992, Contrib. Sci. Nat. Hist. Mus. Los Angeles Co., no. 434, p. 37, figs. 106, 107.

Plicatula filamentosa concentrica DALL, 1898, Trans. Wagner Free Inst. Sci. Phila., v. 3, pt. 4, p. 762; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 281; DOCKERY, 1980, Mississippi Dept. Nat. Res., Bull. 122, p. 158, pl. 47, figs. 6, 8.

Plicatula filamentosa planata MEYER and ALDRICH, 1886, Cincinnati Soc. Nat. Hist., Jour., v. 9, no. 2, p. 45, pl. 2, fig. 20; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 281; TOULMIN, 1977, Geol. Survey Alabama, Monograph 13, p. 260, pl. 40, fig. 12; DOCKERY, 1980, Mississippi Dept. Nat. Res., Bull. 122, p. 158, pl. 23, fig. 6, pl. 48, figs. 1-3.

Discussion: Kellum (1926) reported *Plicatula filamentosa* Conrad (1833) from the Castle Hayne Limestone. Palmer and Brann (1965) listed his record as an undescribed species, not the Claibornian *P. filamentosa.* Kellum's figured specimen and the Santee and Castle Hayne Limestone specimens in the present study are conspecific with *P. filamentosa,* most closely resembling the nominate form rather than *P. filamentosa concentrica* Dall, 1898, or *Plicatula filamentosa planata* Meyer and Aldrich, 1886. The latter two are reported to occur together (Palmer and Brann, 1965). Dall (1898) noted that *P. filamentosa concentrica* intergrades with *P. filamentosa* s.s., so these "subspecies" must be regarded as varieties.

The Early Eocene specimen from Baja California figured by Squires and Demetrion (1992) closely resembles figures of *P. filamentosa "concentrica"* in Harris (1919, pl. 12, fig. 10) and in Dockery (1980, pl. 47, figs. 6-8). Also within the range of *P. filamentosa* s.l. (as figured by Harris, 1919) are four specimens from the Ocala Group figured by Harris (1951). Two of these figures (Harris, 1951, pl. 2, figs. 6, 7) also appear in Richards (1955b, first pl., figs. 2-3). The epifaunal cemented growth form of this genus produces wide variations in shell morphology. This species is present at SAO, MMB, SAJ, and MMG.

Subclass HETEROCONCHIA
Order VENEROIDA
Superfamily CARDITOIDEA
Family CARDITIDAE
Genus GLYPTOACTIS Stewart, 1930

GLYPTOACTIS (CLAIBORNICARDIA) ALTICOSTATA (Conrad)
Plate 3, figure 4

Cardita alticostata CONRAD, 1833, Amer. Jour. Sci., 1st ser., v. 23, no. 2, p. 342; RICHARDS, 1968, Acad. Nat. Sci. Phila., Spec. Publ. 8, p. 31.

Venericardia alticostata (Conrad). ?VAUGHAN *in* VEATCH and STEPHENSON, 1911, Georgia Geol. Soc., Bull. 26, p. 240; ?RICHARDS, 1955, Georgia Mineral Newsletter, v. 8, no. 3, p. 113, 115, fig. 9; ?CHEETHAM, 1962, Micropaleontology, v. 8, no. 3, p. 323; TOULMIN, 1969, Trans. Gulf

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PLATE 4

1. *Crassatella eutawcolens,* paratype of *C. inglisia,* calcite cast, FGS loc. L-92; FGS I-7542; 24.1 mm (l).
2. *Crassatella eutawcolens,* latex cast, SAO; UNC 15441; 51.9 mm (l).
3. *Crassatella eutawcolens,* internal mold, SAO; UNC 15442; 42.7 mm (l).
4. *Crassatella texalta,* internal mold, SAO; UNC 15440; 96.4 mm (l).
5. *Crassatella alta,* internal mold, GP; UNC 15443; 107.1 mm (l).
   Note: In the original figure of FGS I-7542 (Richards and Palmer, 1953, pl. 9, fig. 10), 20.3 mm and 24.1 mm are both listed as the height due to a typographical error. As it is longer than high and because length is consistently listed second, one can safely conclude that 24.1 mm is actually the length.

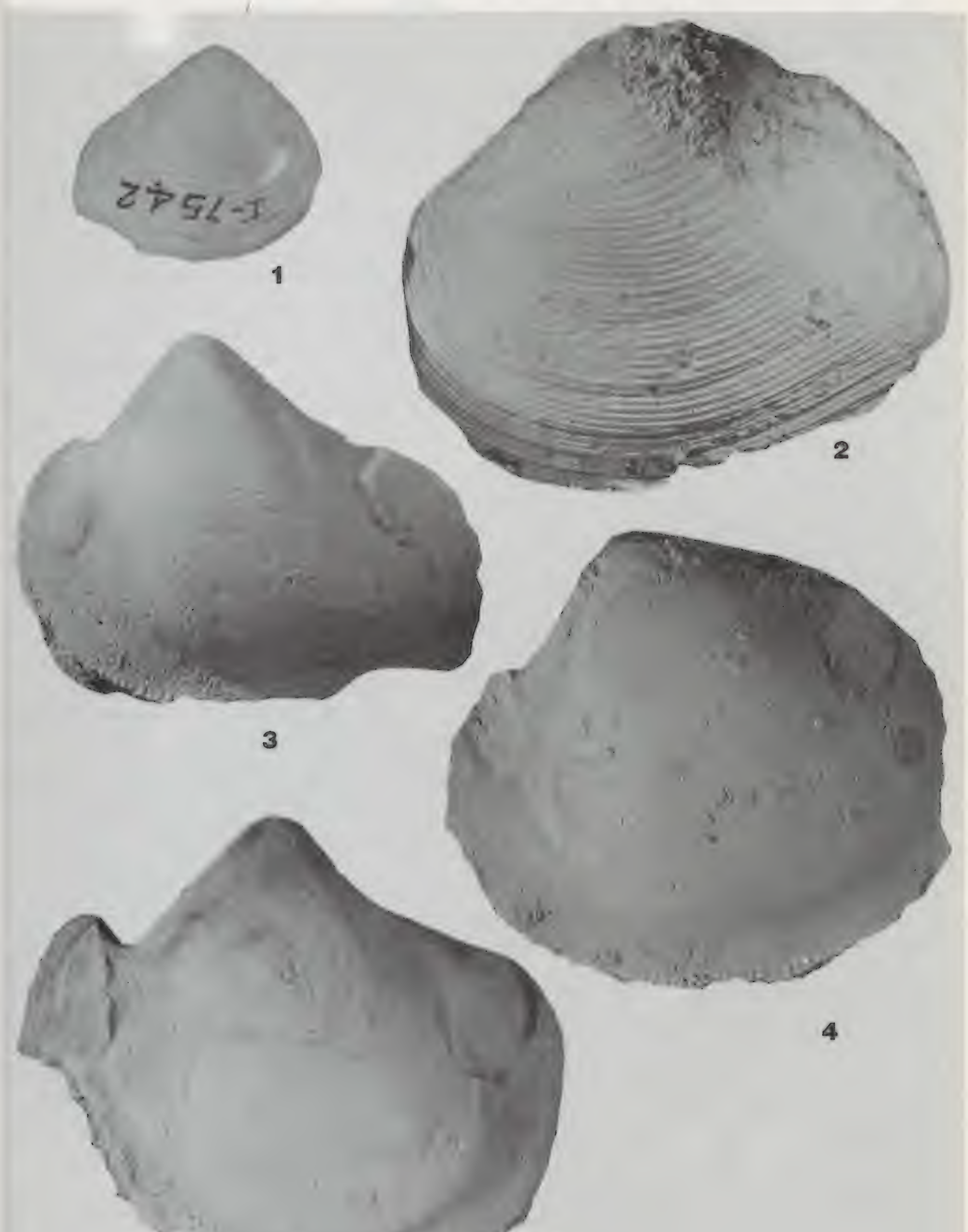

PLATE 4

Coast Assoc. Geol. Soc., v. 19, p. 472, pl. 3, figs. 7, 8.

?*Venericardia* sp. aff. *V. alticostata* (Conrad). COOKE and MACNEIL, 1952, U.S. Geol. Survey, Prof. Paper 243-B, p. 24

Venericardia (Claibornicardia) alticostata (Conrad). STENZEL, KRAUSE, and TWINING, 1957, Univ. of Texas, Publ. 5704, p. 8, 104, pl. 13, figs. 1-9, pl. 14, fig. 5 (type of *Claibornicardia*); PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 321, pl. 2, figs. 10, 11; HEASLIP, 1968, Paleontographica Amer., v. 6, no. 39, p. 55 *et seq.*, pl. 26, figs. 6-11; TOULMIN, 1977, Geol. Survey Alabama, Monograph 13, p. 263, 356, pl. 41, figs. 8-10.

?*Venericardia* cf. *V. nasuta* Dall. POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1105.

Glyptoactis (Claibornicardia) alticostata (Conrad). CHAVAN, 1969, *in* R. C. MOORE (ed.), Treatise on Invertebrate Paleontology, Part N, Mollusca 6, v. 2. p. N557; NYSTROM, WILLOUGHBY, and DOCKERY, 1990, Proc. Second Bald Head Island Conf. (conference version), p. 54; DOCKERY and NYSTROM, 1990, *ibid.* (conference version), p. 82, 84, 86; NYSTROM, WILLOUGHBY, and DOCKERY, 1992, *ibid.* (revised version), p. 59; DOCKERY and NYSTROM, 1992, *ibid.* (revised version), p. 90, 92, 95.

Not *Venericardia alticostata* (Conrad). RICHARDS, 1955, Georgia Mineral Newsletter, v. 8, no. 3, p. 112.

(Additional synonyms in Heaslip, 1968)

Discussion: Glyptoactis (Claibornicardia) alticostata traditionally has been considered indicative of latest Claibornian age (correlating with the Gosport Sand). Before 1992, it was reported with adequate documentation only from the Gosport Sand (above the last regional occurrence of *Cubitostrea sellaeformis*) and from the Orangeburg District Beds of South Carolina. Its presence in these beds, along with the absence of *Cubitostrea sellaeformis*, are major reasons for the post-*C. sellaeformis* zone Gosport Sand equivalence proposed by Dockery and Nystrom (1992a, 1992b).

However, *G. alticostata* is also found in the Santee Limestone at MMB and SAO, along with *C. sellaeformis*. Both are abundant and are often found in the same boulder. Hence, at least one of these taxa had a longer chronological range in South Carolina than in the Gulf Coast. Because of the greater affinities of the Santee Limestone fauna to the *C. sellaeformis* zone beds of the Gulf Coast (upper Lisbon Formation, Cook Mountain Formation) than to the Gosport Sand, it is probably *G. alticostata* that appeared earlier in the Santee Limestone than in the Gulf, as suggested by Dockery and Nystrom (1992a, 1992b), and not a diachronous extinction of *C. sellaeformis*. *Glyptoactis alticostata* is, therefore, not a valid index species for uppermost Claibornian age in all deposits. As discussed above, Dockery and Nystrom (1992a) suggested that the boundary between carbonate and clastic environments acted as an environmental barrier to the spread of this species until the latest Claibornian. Specimens in this study came from MMB, SAO, MMG, SAJ, and Dockery and Nystrom (1992a) locality 25.

Vaughan (*in* Veatch and Stephenson, 1911) reported both *C. sellaeformis* (as *Ostrea*) and *G. alticostata* (as *Venericardia*) from the type locality of the "McBean Formation." However, the labeled specimens of both species from this collection are juveniles, which are difficult to identify. Richards (1955a) lists both species from the Wilcox Group in Georgia (middle Paleocene to lowermost Eocene), probably based on early records that lumped other taxa under these names. His report of *G. alticostata* in the Claibornian of Georgia is possible, but the figure (p. 115, fig. 9) is not clear and may be a comparison specimen from Alabama.

PLATE 5

1. *Crassatella alta*, latex cast, SAO; UNC 15456; 121.3 mm (l).
2. *Crassatella willcoxi*, holotype, internal mold and calcite cast, Wilmington, N.C.; ANSP 12463; 105 mm (l).
3. *Crassatella willcoxi*, holotype, internal mold, Wilmington, N.C.; ANSP 12463; 105 mm (l).
4. *Lirodiscus smithvillensis*, latex cast, SAO; UNC 15458; 17.5 mm (l).
5. *Chama monroensis*, latex cast, SAO; UNC 15459; 24.4 mm (d).
6. *Chama monroensis*, latex cast, SAO; UNC 15460; 37.1 mm (d).

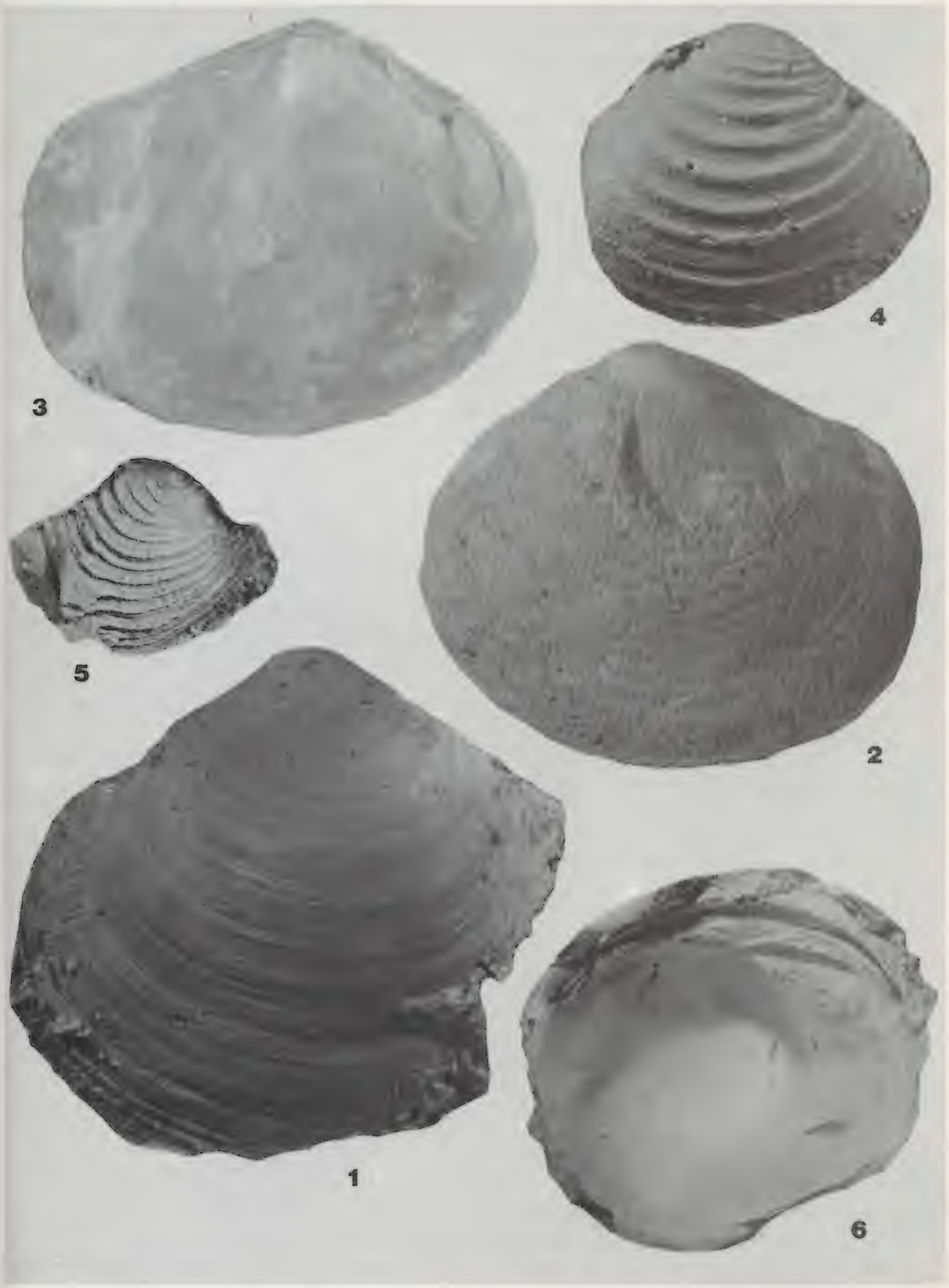

PLATE 5

Superfamily CRASSATELLOIDEA
Family ASTARTIDAE
Genus LIRODISCUS Conrad, 1869

LIRODISCUS SMITHVILLENSIS (Harris)
Plate 5, figure 4

Astarte smithvillensis HARRIS, 1895, Acad. Nat. Sci. Phila., Proc., v. 47, p. 48, pl. 1, figs. 8, 8a, 9-9c.

Lirodiscus smithvillensis (Harris). HARRIS, 1919, Bulls. Amer. Paleontology, v. 6, p. 89, pl. 31, figs. 17-23; HARBISON, 1944, Acad. Nat. Sci. Phila., Not. Nat., no. 143, p. 4; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 177.

Lirodiscus santeensis HARBISON, 1944, Acad. Nat. Sci. Phila., Not. Nat., no. 143, p. 4, pl. 2, fig. 3; ?COOKE and MACNEIL, 1952, U.S. Geol. Survey, Prof. Paper 243-B, p. 24; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 177; RICHARDS, 1968, Acad. Nat. Sci. Phila., Spec. Publ. 8, p. 82.

?*Lirodiscus* sp. BAUM *et al.*, 1980, South Carolina Geology, v. 24, no. 1, p. 25; POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1105.

Lirodiscus (Lirodiscus) cf. *L. (L.) smithvillensis* (Harris). DOCKERY, 1980, Mississippi Dept. Nat. Res., Bull. 122, p. 174, pl. 50, figs. 2, 3.

Discussion: Comparison of latex casts from SAO with the original figure of *Lirodiscus santeensis* and with the original figure of *L. smithvillensis* shows that all three are conspecific. In the original description, Harris (1895) noted the variability of this species. The "larger size, the closer interspaces, the more rounded margin, and the wider diameter," cited by Harbison as distinguishing the two species, do not appear to be valid differences. Harbison's specimen is incomplete, so the roundness of the margin is indeterminate. Reconstructing the margin gives a diameter of 25 mm *versus* 17 mm for Harris's largest figured specimen. The interspaces also appear similar. Specimens in this study came from SAO.

Family CRASSATELLIDAE
Genus CRASSATELLA Lamarck, 1799

CRASSATELLA EUTAWCOLENS (Harris)
Plate 4, figures 1-3

?"*Crassatella,* agreeing with a cast from Eutaw" LYELL, 1845, Quart. Jour. Geol. Soc. London, Proc., v. 1, p. 431.

Crassatellites eutawcolens HARRIS *in* VAN WINKLE and HARRIS, 1919, Bulls. Amer. Paleontology, v. 8, p. 14, pl. 2, fig. 4.

Crassatellites species "a" KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 11, 22, pl. 3, fig. 1.

Crassatella sp. [second]. HARRIS, 1951, Bulls. Amer. Paleontology, v. 8, no. 138, p. 19 [in part], pl. 8, fig. 12; PALMER and BRANN, 1965, *ibid.*, v. 48, p. 107 [in part].

Crassatella eutawcolens (Harris). PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 100.

Crassatella inglisia RICHARDS *in* RICHARDS and PALMER, 1953, Florida Geol. Survey, Bull. 35, p. 46, pl. 9, figs. 9, 10; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 101.

Crassatellites sp. ?BAUM *et al.*, 1980, South Carolina Geology, v. 24, no. 1, p. 25.

Crassatella aff. *C. texana* Heilprin. J. CARTER *et al.*, 1988, North Carolina Geol. Survey, Bull. 89, pl. 4, figs. 24, 25 [not *C. texana* Heilprin, 1891].

Not *Crassatellites* species "a" Kellum. HARBISON, 1944, Acad. Nat. Sci. Phila., Not. Nat., no. 143, p. 4, pl. 2, fig. 1.

"Crassatellinae" BAUM, 1980, Southeastern Geol., v. 21, no. 3, p. 195 [in part?].

Discussion: The distinctive, somewhat rectangular shape of *Crassatella eutawcolens* (Harris *in* Van Winkle and Harris, 1919) also characterizes *Crassatellites* sp. "a" of Kellum, both known only as internal molds. Harbison's (1944) *Crassatellites* sp. "a" is actually a lucine. Harris (1951, pl. 8, fig. 12) figured an internal mold of this species from the Ocala Limestone as the rhomboidal end of variation in a series of molds. In addition, molds found in this study show that this peculiar internal form has the exterior sculpture shown by *Cras-*

PLATE 6

1. *Clavilithes abruptus?,* internal mold, SAO; UNC 15470; 82.1 mm (h).
2. *Santeevoluta wilmingtonensis,* latex cast, SAO; UNC 15462; 149.5 mm (h).
3. *Hippochrenes fissura,* original shell, Calcaire Grossier, France; USNM 496700; 87.5 (h).
4. *Santeevoluta wilmingtonensis,* latex cast, SAO; UNC 15461; 34.8 mm (h) in photo, entire specimen 180.8 mm.

PLATE 6

satella inglisia Richards, 1953, which is based on calcite casts of the external form. J. Carter *et al.* (1988) figured a calcite cast of a left valve that replicates the external sculpture and much of the internal form precisely. Thus, *Crassatella eutawcolens* has been found in limestone deposits from North Carolina to Florida by several workers since Harris, but has gone largely unrecognized. This species is present at MMG, SAJ, and SAO.

The original figure of *Crassatella rhomboidea* (Conrad, 1846) suggests a broken mold of this species; however, the holotype is actually a complete internal mold of a distinct species with very low beaks.

Crassatella texalta Harris
Plate 4, figure 4

Crassatella texalta HARRIS, 1895, Acad. Nat. Sci. Phila., Proc., v. 47, p. 49, pl. 2, fig. 2; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 104; TOULMIN, 1977, Geol. Survey Alabama, Monograph 13, p. 247, pl. 34, figs. 3, 4; DOCKERY, 1980, Mississippi Dept. Nat. Res., Bull. 122, p. 175, pl. 23, fig. 1, pl. 50, figs. 1, 4, pl. 51, figs. 1, 5-7.

Crassatella cf. *C. texalta* Harris. ?BAUM, HARRIS, and ZULLO, 1979, *in* G.R. BAUM, W.B. HARRIS, and V.A. ZULLO (eds.), Structural and Stratigraphic Framework for the Coastal Plain of North Carolina, p. 108; ?BAUM *et al.*, 1980, South Carolina Geology, v. 24, no. 1, p. 23, 25; ?POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1102, 1105.

Crassatellites alta (Conrad) KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 8, 11, 22 [in part?].

Discussion: Three species of very large crassatellids with roughly equal height and length are present in the Santee Limestone and "Cross Formation." *Crassatella texalta* Harris, 1895, is reported from various upper Claibornian (Cook Mountain Formation equivalent) localities. It is most easily distinguished from *Crassatella alta* Conrad, 1832 by the lack of concentric undulations in the umbonal area, which are present in *C. alta*. As noted by Harris (1919), *Crassatella willcoxi* (Brown and Pilsbry, 1912) continues this trend by having concentric undulations over the entire shell.

An external mold of *C. texalta* from the SAO quarry preserved the lack of umbonal sculpture. The lateral profiles of the three species and their pallial lines also differ. Harris (1919) further observed that *C. texalta* is more angular as an adult than is *C. alta*. The maximum known size of *C. texalta* is less than that of *C. alta*, but *C. willcoxi* reaches as large a size as *C. alta*. *Crassatella texalta* is present at SAO and MMB.

Crassatella alta Conrad
Plate 4, figure 5; Plate 5, figure 1

Crassatella alta CONRAD, 1832, Fossil shells of the Tertiary formations of North America, v. 1, no. 2, p. 21, pl. 7; ?RICHARDS, 1950, Amer. Philos. Soc., Trans., n. s., v. 40, pt. 1, p. 18; COOKE and MACNEIL, 1952, U.S. Geol. Survey, Prof. Paper 243-B, p. 25 [in part?]; ?CHEETHAM, 1961, Jour. Paleontology, v. 35, no. 2, p. 395; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 98; POOSER, 1965, Univ. Kansas Paleont. Cont., Arthropoda, art. 8, p. 18 [in part]; RICHARDS, 1968, Acad. Nat. Sci. Phila., Spec. Publ. 8, p. 31; TOULMIN, 1969, Trans. Gulf Coast Assoc. Geol. Soc., v. 19, p. 474, pl. 3, fig. 9; TOULMIN, 1977, Geol. Survey Alabama, Monograph 13, p. 246, pl. 34, figs. 7-9; ?BAUM, HARRIS, and ZULLO, 1979, *in* G.R. BAUM, W.B. HARRIS, and V.A. ZULLO (eds.), Structural and Stratigraphic Framework for the Coastal Plain of North Carolina, p. 11; ?BAUM *et al.*, 1979, *ibid.*, p. 89, 91; ?WARD *et al.*, 1979, South Carolina Geol. Notes, v. 23, p. 8, 12, 29, 31; ?WARD and BLACKWELDER, 1980, *in* R.W. FREY (ed.), Excursions in Southeast-

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PLATE 7

1. *Strombus alatus*, original shell, Recent, Florida; UNC 15464; 81.7 mm (h).
2. *Hystrivasum locklini*, original shell, APAC pit, Sarasota, Florida; UNC 15465; 100.5 mm (h).
3. *Scaphella trenholmi*, original shell, Pliocene, North Carolina; UNC 15466; 106.4 mm (h).
4. *Santeevoluta wilmingtonensis*, holotype, internal mold, Wilmington, N.C.; ANSP 13476; 113 mm (h).
5. *Santeevoluta wilmingtonensis, holotype*, internal mold, Wilmington, N.C.; ANSP 13476; 113 mm (h).

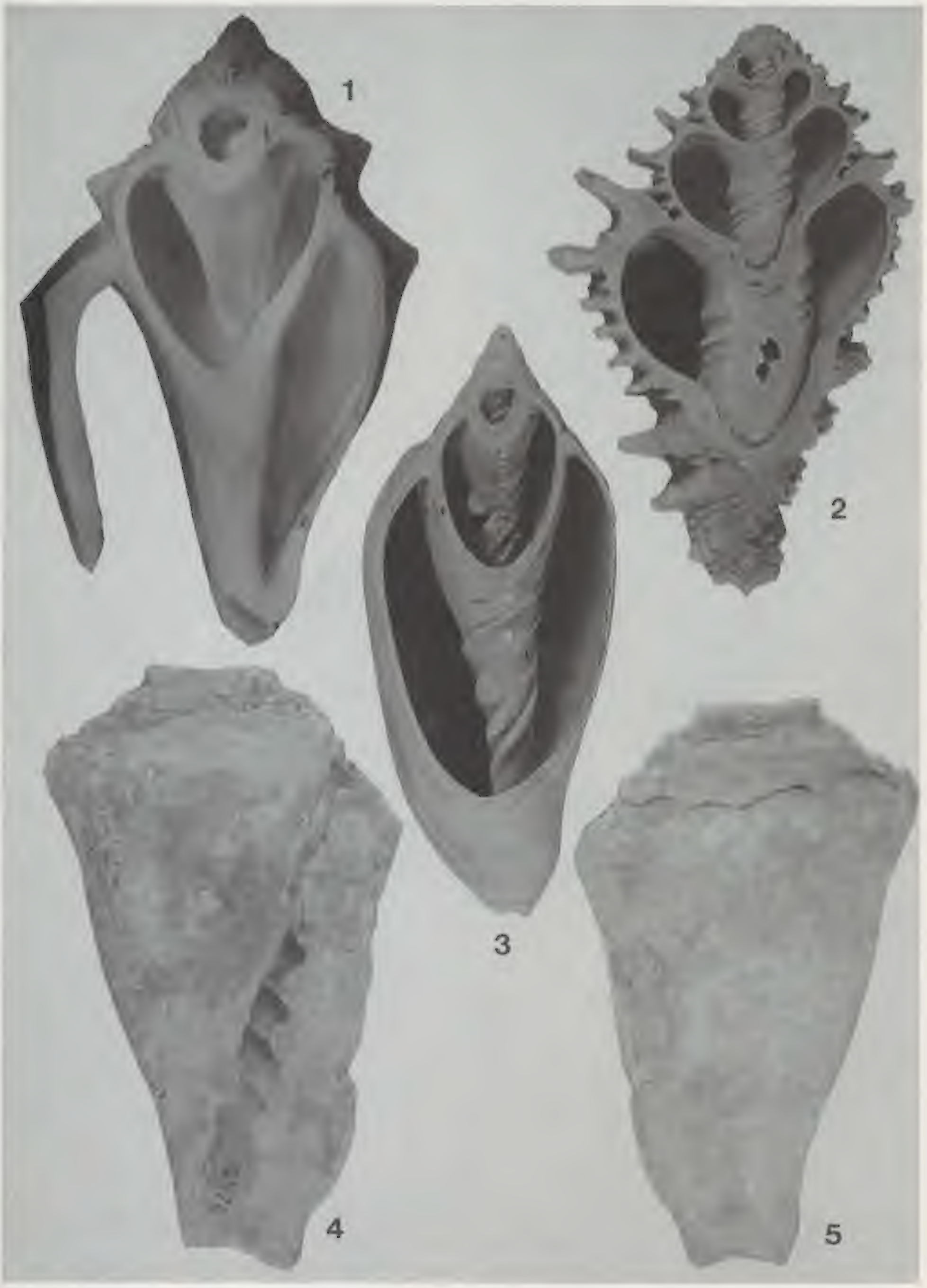

PLATE 7

ern Geol., v. 1, p. 193, 202; ?DUBAR *et al.*, 1980, *ibid.*, v. 1, p. 234, 236; ?BAUM *et al.*, 1980, South Carolina Geology, v. 24, no. 1, p. 19, 23; ?HARRIS and ZULLO, 1980, Geol. Soc. Amer., Bull., v. 91, p. 589; ?POWELL and BAUM, 1982, *ibid.*, v. 93, p. 1101, 1105; ?J. CARTER *et al.*, 1988, North Carolina Geol. Survey, Bull. 89, p. 26; ?NYSTROM, WILLOUGHBY, and DOCKERY, 1990, Proc. Second Bald Head Island Conf. (conference version), p. 56; ?WARD and J. CARTER, 1992, *in* J.M. DENNISON and K.G. STEWART (eds.), Geologic Field Guides to North Carolina and Vicinity, Field Trip 8, p. 118, 123, 127; ?DOCKERY and NYSTROM, 1992, Proc. Second Bald Head Island Conf. (revised version), p. 93.

Crassatellites altus (Conrad). ?GARDNER *in* MILLER, 1912, North Carolina Geol. and Econ. Survey, Publ., v. 3, p. 188; ?CLARK, 1912, *ibid.*, v. 3, p. 316.

Crassatellites alta (Conrad). KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 8, 11, 22 [in part?]; ?RICHARDS, 1950, Amer. Philos. Soc., Trans., n. s., v. 40, pt. 1, p. 18.

Crassatella cf. *C. alta* (Conrad) ?BAUM, HARRIS, and ZULLO, 1978, Southeastern Geol., v. 20, no. 1, p. 11; ?BAUM, HARRIS, and ZULLO, 1979a, *in* G.R. BAUM, W.B. HARRIS, and V.A. ZULLO (eds.), Structural and Stratigraphic Framework for the Coastal Plain of North Carolina, p. 9; ?BAUM, HARRIS, and ZULLO, 1979, *ibid.*, p. 101; ?BAUM, 1980, Southeastern Geol., v. 21, no. 3, P. 195; ?BAUM, 1981, *ibid.*, v. 22, no. 4, p. 181.

Discussion: Crassatella alta, like *Glyptoactis alticostata*, is a traditional index species for the uppermost Claibornian that also occurs in older deposits in the Santee Limestone. Many stratigraphic works on the Santee and Castle Hayne limestones (Cooke and MacNeil, 1952; Pooser, 1965; Ward *et al.*, 1979; Baum *et al.*, 1980; Ward and Blackwelder, 1980; Powell and Baum, 1982) cite abundant *C. alta* as indicative of uppermost Claibornian age (Gosport Sand equivalent) deposits, now referred to the "Cross Formation" and the New Bern Formation or Spring Garden Member of the Castle Hayne Limestone. *Crassatella alta* was listed by Baum *et al.* (1979) as another taxon causing much biostratigraphic confusion in the Eocene of the Carolinas. In this study, *C. alta* was found in the "Cross Formation" at GP and the Santee Limestone at SAO. *Crassatella alta* and *C. texalta* are both found at SAO, and Dockery and Nystrom (1992a, 1992b) also reported *C. alta* from the Santee Limestone at MMB. The similarity of these two species makes careful identification necessary.

CRASSATELLA WILLCOXI
Brown and Pilsbry
Plate 5, figures 2, 3

Crassatellites willcoxi BROWN and PILSBRY, 1912, Acad. Nat. Sci. Phila., Proc., v. 64, p. 152, pl. 1, fig. 1; HARRIS, 1919, Bulls. Amer. Paleontology, v. 6, p. 104; RICHARDS, 1950, Amer. Philos. Soc., Trans., n. s., v. 40, pt. 1, p. 74, fig. 61a (as *wilcoxi* lapsus calami); RICHARDS, 1968, Acad. Nat. Sci. Phila., Spec. Publ. 8, p. 96.

Crassatella wilcoxi [sic] (Brown and Pilsbry). RICHARDS, 1950, Amer. Philos. Soc., Trans., n. s., v. 40, pt. 1, p. 18; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 105.

?*Crassatellites* species "b" KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 11, 23, pl. 3, fig. 2; HARBISON, 1944, Acad. Nat. Sci. Phila., Not. Nat., no. 143, p. 4.

Crassatellites negreetensis HARRIS, 1919, Bulls. Amer. Paleontology, v. 6, p. 97 [in part?], ?pl. 33, figs. 6-8.

Crassatella negreetensis (Harris). PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 102 [in part?].

Discussion: The type of *Crassatella willcoxi* is an exceptionally good specimen for the Castle Hayne Limestone in that it preserves a complete internal mold with a partial cast of the external sculpture. *Crassatellites* species "b" of Kellum is probably the young of this species, but it could be *Crassatella texalta* or *C. alta*. In addition to

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PLATE 8

1. *Santeevoluta wilmingtonensis*, internal and external mold, SAO; UNC 15471; internal mold, 172 mm (h); external mold, 220 mm (h).
2. *Santeevoluta wilmingtonensis*, internal mold, MMB; UNC 8223; 166.1 mm (h).
3. *Santeevoluta wilmingtonensis*, composite latex casts, SAO; UNC 15454, UNC 15455. Apical portion: 110.0 mm (h), 132.1 mm (w); body whorl 119.5 mm (h).
4. *Santeevoluta wilmingtonensis*, latex cast, SAO; UNC 15463; 35.2 mm (h).

PLATE 8

its more extensive sculpture, *C. willcoxi* is more elongate as an adult than either of the other two species. *Crassatella negreetensis* (Harris, 1919) may be a junior synonym from the Gulf Coast. The specimens from Eutaw Springs, S.C., tentatively assigned to *C. negreetensis* by Harris (1919) and Palmer and Brann (1965) are probably *C. willcoxi*, even if the Gulf Coast form is validly distinct. This species is common at MMG and SAJ and rare at SAO. Its abundance at these two localities and near Wilmington, N.C., suggests that it favored deeper water than *C. texalta* or *C. alta*.

Superfamily CHAMOIDEA
Family CHAMIDAE
Genus CHAMA Linnaeus, 1758
CHAMA MONROENSIS Aldrich
Plate 5, figures 5, 6

Chama monroensis ALDRICH, 1903, Nautilus, v. 16, no. 9, p. 100, pl. 4, fig. 15; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 79; DOCKERY, 1980, Mississippi Dept. Nat. Res., Bull. 122, p. 166, pl. 48, figs. 4, 5, 8.

Chama sp. "a" KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 11, 23, pl. 3, fig. 5; HARBISON, 1944, Acad. Nat. Sci. Phila., Not. Nat., no. 143, p. 5; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 80; ?POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1105.

Chama richardsi HARBISON, 1944, Acad. Nat. Sci. Phila., Not. Nat., no. 143, p. 5, pl. 2, figs. 5, 6; PALMER and BRANN, 1965, Bulls. Amer. Paleontology, v. 48, p. 79; RICHARDS, 1968, Acad. Nat. Sci. Phila., Spec. Publ. 8, p. 81; POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1105.

Chama sp. BAUM *et al.*, 1980, South Carolina Geology, v. 24, no. 1, p. 25; BAUM, 1980, Southeastern Geol., v. 21, no. 3, p. 194.

Discussion: Chama richardsi is an internal mold of *Chama monroensis*, as shown by combinations of molds showing both sides of a single valve. Also, all external molds of *Chama* in the present collections from the Santee Limestone are assignable to *C. monroensis*. These external molds are similar in size to the "*C. richardsi*" internal molds. Harbison contrasted *C. richardsi* with *Chama* sp. "a" of Kellum. The posterior margin of Kellum's figured specimen is somewhat irregular, indicating that it is slightly incomplete. Harbison differentiated the two on the basis of the appearance of the posterior portion of the molds. No difference is evident between Kellum's and Harbison's specimens. This species is present at MMB and SAO.

Class GASTROPODA
Subclass PROSOBRANCHIA
Order MESOGASTROPODA
Superfamily TONNOIDEA
Family FICIDAE
Genus FICUS Röding, 1798
FICUS AFFINIS Van Winkle
Plate 9, figure 1

Ficus affinis VAN WINKLE *in* VAN WINKLE and HARRIS, 1919, Bulls. Amer. Paleontology, v. 8, p. 8, pl. 1, figs. 10, 10a; PALMER and BRANN, 1966, *ibid.*, v. 48, p. 680.

Not *Ficus* sp. PALMER and BRANN, 1966, Bulls. Amer. Paleontology, v. 48, p. 681.

Discussion: Ficus affinis was originally described from the bank of the James River, just below City Point in Virginia. It is also represented in the present collections from Dockery and Nystrom's locality 25 (silicified) and SAO. These finds are of stratigraphic significance, because they suggest that this species came from the upper Claibornian Piney Point Formation and not the upper Sabinian Nanjemoy Formation, to which Palmer and Brann (1966) referred the City Point locality. Because the Nanjemoy Formation was the main fossiliferous formation known from the Paleogene of Virginia at that time, the age assignment was reasonable. However, fossiliferous beds of the Piney Point Formation are now known to outcrop in this area (Ward, 1985), making it a likely source for this species. A previous report of *Ficus*

PLATE 9

1. *Ficus affinis*, latex cast, SAJ; UNC 15232; 18.8 mm (h).
2. *Voluticella levensis*, latex cast, SAO; UNC 15467; 23.9 mm (h).
3. *Voluticella levensis*, latex cast, SAO; UNC 15445; 47.5 mm (h).
4. *Voluticella levensis*, latex cast, SAO; UNC 15467; 23.9 mm (h).
5. *Conus smithvillensis* var., latex cast, SAO; UNC 15448; 27.6 mm (h).

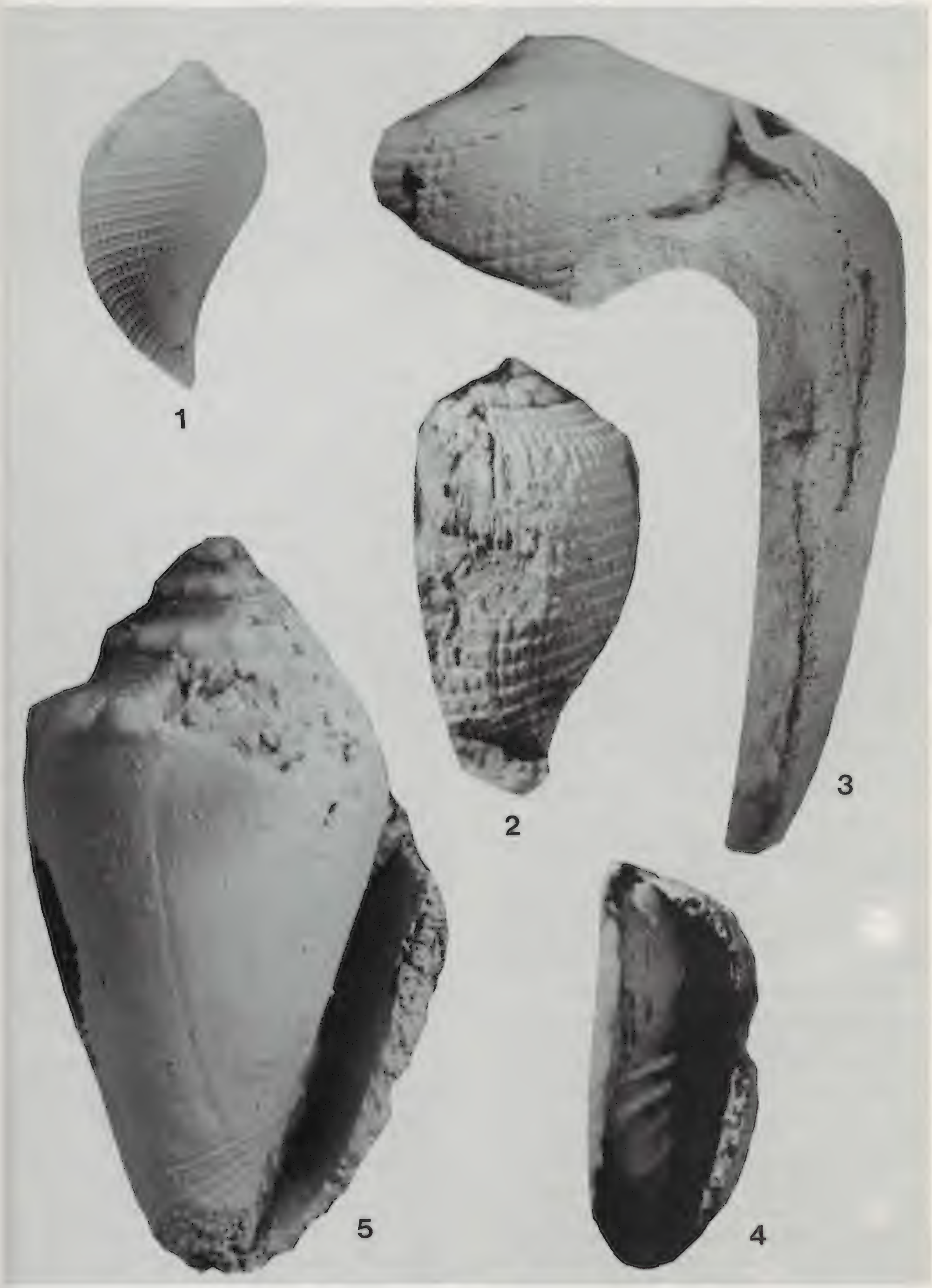

PLATE 9

sp. from the Castle Hayne Limestone (a reassignment of *Cassis* ? sp. of Kellum, 1926) proves to be *Ficopsis penita* (Conrad, 1833).

Order NEOGASTROPODA
Superfamily BUCCINOIDEA
Family FASCIOLARIIDAE
Genus CLAVILITHES Swainson, 1840

?CLAVALITHES ABRUPTUS (Tuomey)

Plate 6, figure 1

?*Fusus abruptus* TUOMEY, 1853, Acad. Nat. Sci. Phila., Proc., v. 6, p. 193.

Fusinus abruptus (Tuomey). KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 8, 11, 29, pl. 6, fig. 1 [not fig. 6 as in PALMER and BRANN, 1966]; HARBISON, 1944, Acad. Nat. Sci. Phila., Not. Nat., no. 143, p. 6, pl. 4, fig. 1; ?RICHARDS, 1950, Amer. Philos. Soc., Trans., n. s., v. 40, pt. 1, p. 18; ?DUBAR *et al.*, 1980, *in* R.W. FREY (ed.), Excursions in Southeastern Geol., v. 1, p. 234, 236; ?POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1105; ?J. CARTER *et al.*, 1988, North Carolina Geol. Survey, Bull. 89, p. 26; ?WARD and J. CARTER, 1992, *in* J.M. DENNISON and K.G. STEWART (eds.), Geologic Field Guides to North Carolina and Vicinity, Field Trip 8, p. 123.

Fusinus sp. KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 11, 29, pl. 6, fig. 2; COOKE and MACNEIL, 1952, U.S. Geol. Survey, Prof. Paper 243-B, p. 26.

?Cf. *Clavilithes abruptus* (Tuomey). PALMER and BRANN, 1966, Bulls. Amer. Paleontology, v. 48, p. 583.

Discussion: Although Tuomey (1853) described *Fusus abruptus* rather briefly without a figure ("ovoid; whorls rounded, ventricose, the last one terminating abruptly in the canal. Dimen. Spiral angle 70°; ht. 6 in; br. 4 in."), it is frequently reported in the subsequent literature. Kellum (1926, p. 29) stated that, although the specimens he collected from the type locality suggested a smaller spire angle than Tuomey's estimate, they were fairly common and were "the only large *Fusus*-like forms" present. On these grounds, Kellum thought his species was probably what Tuomey had in mind, though he doubted that it could be definitively identified. Palmer and Brann (1966) tentatively assigned *Fusus abruptus* to *Clavilithes* and questioned other records, probably because of the inadequate original description and lack of a known type. The records after Tuomey are probably all assignable to *Clavilithes* spp. Kellum (1926) and Harbison (1944) had the same species, also present in the Banks and Powell collections and in my material from MMB and SAO, but it is uncertain if this is Tuomey's species, which is probably best regarded as a *nomen dubium*. Unfortunately, Harbison's figured specimen is probably lost. A note with the collections at the Academy of Natural Sciences at Philadelphia in Axel Olsson's handwriting states that it was removed for a temporary exhibit, which would have been about 1960.

Superfamily VOLUTOIDEA
Family VOLUTIDAE
Genus SANTEEVOLUTA gen. nov.

Description: Protoconch low for a volutid, domed, paucispiral; spire proportionally short, nodose, rapidly expanding; large (›250 mm maximum length); body whorl smooth below shoulder except for irregular growth lines, roughly conical; parietal callous present; four prominent columellar plaits; lip broad, flaring, recurved.

Type species: Vasum wilmingtonense Brown and Pilsbry, 1912.

Stratigraphic distribution: Castle Hayne Limestone, Santee Limestone.

Etymology: From the Santee Limestone, so that the genus and species names together give the known range of this taxon.

Discussion: Santeevoluta wilmingtonensis, the type species, was originally described as a *Vasum* (Brown and Pilsbry, 1912). Palmer and Brann (1966) questioned the generic assignment, and Vokes (1966) recognized that it was not a *Vasum* but rather a volutid. Lacking a suitable genus, she suggested that it was "a large *Fusimitra*" (Vokes, p. 5), now considered a subgenus of *Mitra* (Dockery, 1980). Species of *Fusimitra,* including the type [*M. (Fusimitra) millingtoni*], are proportionally much narrower than *S. wilmingtonensis,* and have a spire approximately equal in length to the body whorl, whereas the latter has a spire only about one-fourth as long as the body whorl and reaches a much greater size than any known *Fusimitra* (25 *versus* 15 cm).

The shell is too thin and the columellar folds are too strong for a *Vasum* or an *Eovasum.* The flaring lip has no parallel in the Vasidae. *Vasum haitense* (Sowerby, 1850), cited in the original description, has a broad shoulder not found in *Santeevoluta* and is, thus, proportionally broader. It also

shows greater development of sculpture than *Santeevoluta*. *Eovasum* is smaller than *Santeevoluta*, with a row of nodes on the lower body whorl. Species of various strombid genera, including *Strombus* Linnaeus (1758), *Hippochrenes* Montfort (1810) (see plate 6, figure 3), and *Wateletia* Cossmann (1889), may possess a large, flaring lip somewhat similar to this species. The latter two genera, from the Paleogene of Europe, have elongated anterior canals and proportionally taller spires, over half as long as the body whorl (including canal), unlike *Santeevoluta*. *Wateletia geoffroyi* (Watelet, 1855) (the type species) also differs from *Santeevoluta* in having an apical flange extending from the flaring lip parallel to the spire and in having greater development of the parietal callus, which covers the entire apertural side. *Hippochrenes macroptera* (Lamarck, 1803), on the other hand, seems to lack any appreciable callus. Also, these strombid genera lack strong columellar folds. *Strombus*, like *Vasum*, has a much thicker shell as an adult than does *Santeevoluta*.

Broken specimens and molds of juveniles reveal that the early whorls resemble the volutid *Caricella*, the type species of which (*C. pyruloides*) is present in the Santee Limestone. The unusual shape of the body and extremely large size of *Santeevoluta* distinguish it, however. Plate 7 compares the holotype of *S. wilmingtonensis* with a strombid, a vasid, and a volutid. External molds reveal the presence of a large, recurved, flaring lip not found in any other volutid. Two Cenozoic Australian volutids, *Livonia hannafordi* (McCoy, 1866) and *Ericusa macroptera* (McCoy, 1866) have some development of the lip (Darragh, 1988), though not to the extent found in *Santeevoluta*. The protoconch of *Santeevoluta* is lower and more dome-shaped than that of *Ericusa* and quite unlike the globose, offset protoconch of *Livonia*. The whorl shape is also different from these genera, being more straight-sided in *Santeevoluta*. The spire of *Santeevoluta* is proportionally shorter than in these two genera.

Several genera of volutids (notably the bailers, *Melo* and *Cymbium*) have large apertures, but no other recorded volutid has the extreme development of a recurved, flaring lip shown by the external molds. The domed protoconch resembles that of *Caricella* but is more paucispiral. This unique combination of traits leads me to propose the new genus *Santeevoluta* with "*Vasum*" *wilmingtonense* as the type species.

SANTEEVOLUTA WILMINGTONENSIS
(Brown and Pilsbry)
Plate 6, figures 2, 4; Plate 7, figures 4, 5; Plate 8, figures 1-4

Vasum wilmingtonense BROWN and PILSBRY, 1912, Acad. Nat. Sci. Phila., Proc., v. 64, p. 152, pl. 1, figs. 2, 3; KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 7, 8, 11, 30; PALMER and BRANN, 1966, Bulls. Amer. Paleontology, v. 48, p. 1013; VOKES, 1966, Tulane Stud. Geol., v. 5, no. 1, p. 5; RICHARDS, 1968, Acad. Nat. Sci. Phila., Spec. Publ. 8, p. 205.

Strombus sp. ?LYELL, 1845, Quart. Jour. Geol. Soc. London, Proc., v. 1, p. 431; ?GARDNER *in* MILLER, 1912, North Carolina Geol. and Econ. Survey, Publ., v. 3, p. 188; BANKS, 1977, South Carolina Geol. Notes, v. 21, no. 3, p. 142 [in part?]; ?BAUM, HARRIS, and ZULLO, 1979, *in* G.R. BAUM, W.B. HARRIS, and V.A. ZULLO (eds.), Structural and Stratigraphic Framework for the Coastal Plain of North Carolina, p. 108; BAUM *et al.*, 1980, South Carolina Geology, v. 24, no. 1, p. 25 [in part?]; BAUM, 1980, Southeastern Geol., v. 21, no. 3, p. 194 [in part?]; ?DUBAR *et al.*, 1980, *in* R.W. FREY (ed.), Excursions in Southeastern Geol., v. 1, p. 236; POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1106 [in part?]; HOWE, 1987, Rocks and Minerals, July/August, p. 241 [in part?].

?*Scaphella (Eucymba) ocalana* Dall. KELLUM, 1926, U.S. Geol. Survey, Prof. Paper 143, p. 8, 11, 31; [not *Eucymba ocalana* Dall, 1890, nor "*Eucymba ocalana*" of authors = *Eucymba* sp. of Palmer and Brann, 1966].

Volute species [not *Strombus*]. DOCKERY and NYSTROM, 1992, Proc. Second Bald Head Island Conf. (revised version), p. 93.

Discussion: Brown and Pilsbry (1912) described this unusual species from a large, incomplete internal mold from the Castle Hayne Limestone:

> "This form is represented by an internal cast wanting the apical whorls, apparently derived from a species shaped like *V. haitense*. The conic spire diverges at an angle of about 80°, the crown of each whorl being narrowly rounded. The last whorl is much less convex above, being somewhat flattened and sloping to the rounded shoulder. The periphery, viewed from above, is polygonal; the last three angles on the last half whorl are prominent, but several on the first half are barely

perceptible. Below the shoulder the sides taper to the narrow base, are a little swollen midway and contracted below the shoulder and near the base. Four deep furrows indicate as many stout columellar folds in the shell, the lowest one being somewhat smaller. The length of the cast is 113 mm and the greatest diameter 66 mm."

Kellum (1926) noted that the USNM collections contain many molds of this species and correctly assigned it to the Castle Hayne, which Brown and Pilsbry had questioned. Dockery and Nystrom (1992a) recognized that many records of *Strombus* sp. in faunal lists from the Santee Limestone actually represented a "large volute...common in the Martin Marietta Quarry" that "superficially resembles a large *Strombus*." Several specimens have been found in this study, including internal and external molds which, in combination, show the entire shell.

Santeevoluta wilmingtonensis is, as Dockery and Nystrom (1992a) presumed, chiefly responsible for the reports of *Strombus* sp. from the Santee and Castle Hayne Limestones. Specimens of *Santeevoluta* in the Powell collections at the University of North Carolina at Chapel Hill are labeled *Strombus* sp.; however, so are a few other taxa. *Santeevoluta wilmingtonensis* is present at SAO, MMB, and MMG as well as at various North Carolina quarries.

Kellum (1926) tentatively assigned an internal mold of a juvenile volutid less than 1 cm long to *Eucymba ocalana* Dall, 1890. The identity of *E. ocalana* is confused (Palmer and Brann, 1966). Kellum's specimen may be a very young *Santeevoluta wilmingtonensis*.

Genus VOLUTICELLA Palmer
in Richards and Palmer, 1953
VOLUTICELLA LEVENSIS Palmer
Plate 9, figures 2-4

Voluticella levensis PALMER *in* RICHARDS and PALMER, 1953, Florida Geol. Survey, Bull. 35, p. 11, 37, pl. 5, figs. 4-8; PALMER and BRANN, 1966, Bulls. Amer. Paleontology, v. 48, p. 1017.

Discussion: With its pyriform shape and low spire, *Voluticella levensis* superficially resembles *Ficus*, but the sculpture of the former consists of perpendicular grooves instead of threads. Also, the multiple columellar folds show it to be a volutid rather than a ficid. All specimens from South Carolina are from SAO.

The presence of this supposed Ocala Limestone endemic in the Santee Limestone extends its stratigraphic range from the "Inglis Formation" (lower Ocala Limestone in current Florida usage) into the upper Claibornian of South Carolina. Although it is known only from the southeastern United States, Nicol (1991) considered *Voluticella* to have Tethyan affinities. Its presence in the Santee Limestone, along with other taxa of Tethyan affinities [such as *Nayadina (Exputens)* sp. and *Lyrischapa* sp.] suggests that the warm current flowing through the Gulf Trough provided a pathway for warm-water taxa to reach this region.

Superfamily CONOIDEA
Family CONIDAE
Genus CONUS Linnaeus, 1758
CONUS (LITHOCONUS) SMITHVILLENSIS
var. Dockery
Plate 9, figure 5

?*Conus gyratus* MORTON, 1833, Amer. Jour. Sci., 1st ser., v. 24, p. 131, pl. 10, fig. 13; PALMER, 1937, Bulls. Amer. Paleontology, v. 7, no. 32, p. 465; PALMER and BRANN, 1965, *ibid.*, v. 48, p. 596; RICHARDS, 1968, Acad. Nat. Sci. Phila., Spec. Publ. 8, p. 140.

?*Conus* sp. BAUM *et al.*, 1980, South Carolina Geology, v. 24, no. 1, p. 25; POWELL and BAUM, 1982, Geol. Soc. Amer., Bull., v. 93, p. 1105.

Conus (Lithoconus) smithvillensis Harris var. DOCKERY, 1980, Mississippi Dept. Nat. Res., Bull. 122, p. 137, pl. 43, fig. 8.

Discussion: The most common *Conus* in the Santee Limestone has a nodose shoulder and a taller, more tabulate spire than the widespread *Conus (Lithoconus) sauridens* Conrad, 1833. It closely resembles the *C. (L.) smithvillensis* Harris var. of Dockery (1980), both differing from true *C. (L.) smithvillensis* in lacking the extremely tall spire as shown by Palmer's (1937) figured specimen and Harris's (1895) original figure. Further study may provide enough material to determine whether this variety intergrades with typical *C. smithvillensis*.

Harbison's description of *Conus cormacki* as having a nodose shoulder whorl suggests this species; however, it is actually a broken volutid. *Conus gyratus* Morton, 1833, based on an internal mold, closely resembles internal molds of *C.*

smithvillensis var. Because the holotype of *C. gyratus* was collected in South Carolina, it is probably a synonym of *C. smithvillensis* var. However, internal molds of many species of *Conus* do not seem distinctive. *Conus smithvillensis* var. is present at SAO and MMB.

VIII. SUMMARY

The *Cubitostrea sellaeformis*-zone Santee Limestone faunas of South Carolina appear, on the basis of their molluscan faunas, to be upper Claibornian, coeval with the Cook Mountain Formation of Texas, Louisiana, and Mississippi, the upper Lisbon Formation of Alabama, much of the Castle Hayne Limestone in North Carolina, and the Piney Point Formation of Virginia. The "Cross Formation" at the Giant Portland quarry probably includes both Gosport Sand and Moodys Branch Formation equivalent beds, but is inadequately documented.

Further study of the Eocene deposits of the Atlantic Coastal Plain is needed before reliable regional biostratigraphic markers can be identified. In particular, better understanding of macrofossil evolutionary lineages and more extensive microfossil data will provide improved correlations for the region.

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X. APPENDIX: PRELIMINARY LIST OF MOLLUSCA FROM THE SANTEE LIMESTONE AND "CROSS" FORMATION

For locality information see Text-fig. 2. GP = Giant Portland Quarry; SAO = Southern Aggregates Orangeburg Quarry; MMB = Martin Marietta Berkeley Quarry; MMG = Martin Marietta Georgetown Quarry; SAJ = Southern Aggregates Jamestown Quarry.

Nucula sp. . . . . SAO
Nuculana trumani . . . . . SAO
Arcoperna sp. . . . . SAO
Modiolus cawcawensis . . . . . SAO, MMG
Lithophaga sp. cf. *L. claibornensis* . . . . . SAO
Barbatia (Plagiarca) rhomboidella . . . . . SAO
Barbatia sp. . . . . SAO, MMB, MMG, SAJ
Pachecoa sp. . . . . SAO
Glycymeris sp. . . . . SAO
Glycymeris staminea . . . . . SAO, GP
Lima sp. . . . . SAO, SAJ
Eburneopecten calvatus . . . . . SAO, MMB
Chlamys burlesonensis . . . . . SAO, MMB
Chlamys cawcawensis . . . . . SAO
Chlamys membranosa s.l. . . . . SAO, MMB
Chlamys wahtubbeana s.l. . . . . SAO, MMB
Chlamys (Aequipecten) sp. . . . . GP
Chlamys spp. . . . . MMG, SAJ, GP
Batequeus ducenticostatus . . . . . GP
Spondylus lamellacea . . . . . SAO, MMB
Pteria sp. indet. . . . . SAO
Atrina sp. . . . . SAO, MMG?
Nayadina (Exputens) sp. . . . . MMG
Lopha ["Alectryonia"] ludoviciana . . . . . SAO, MMB
Cubitostrea sellaeformis . . . . . SAO, MMB
Pycnodonte trigonalis . . . . . GP
Pycnodonte sp. . . . . SAJ
Plicatula filamentosa . . . . . SAO, MMB, MMG, SAJ
Diplodonta ungulina . . . . . SAO
Eophysema sp. . . . . GP
Chama monroensis . . . . . SAO, MMB
Venericardia (Venericor) claiboplata . . . . . SAO, MMB
Venericardia (Rotundicardia) eutawcolens . . . . . SAO
Venericardia (Rotundicardia) rotunda . . . . . SAO
Glyptoactis (Claibornicardia) alticostata . . . . . SAO, MMB, MMG, SAJ
Glyptoactis (Claibornicardia) complexicosta . . . . . SAO, MMB
Pleuromeris parva . . . . . SAO
Lirodiscus smithvillensis . . . . . SAO
Lirodiscus (Crustuloides) sp. . . . . SAO, MMG
Crassatella willcoxi . . . . . SAO, MMG, SAJ
Crassatella eutawcolens . . . . . SAO, MMG, SAJ?
Crassatella texalta . . . . . SAO, MMB
Crassatella alta . . . . . SAO, GP
Crassatella sp. . . . . SAO
Agnocardia claibornensis . . . . . SAO
Spisula (Symmorphomactra) praetenuis . . . . . SAO
S. (Symmorphomactra) praetenuis australina . . . . . SAO
Spisula decisa palmaris . . . . . SAO
Gari eborea . . . . . SAO
Semele australina . . . . . SAO
Semele linosa . . . . . SAO, MMB
Eosolen sp. . . . . SAO
Meiocardia carolinae . . . . . SAO, MMB
Callista aequora . . . . . SAO

Callista perovata . . . . . SAO
Callista perovata lisbonensis . . . . . SAO, GP?
Pitar poulsoni . . . . . SAO
Corbula (Caryocorbula) densata . . . . . GP
Caestocorbula wailesiana . . . . . GP
Gastrochaena sp. . . . . MMB
Pholadomya harrisi . . . . . MMB
Pholadomya spp. . . . . SAO, SAJ
Diodora tenebrosa antica . . . . . SAO
Puncturella (Altrix) altior . . . . . SAO, MMB
Turritella arenicola . . . . . SAO, GP
Turritella ghigna . . . . . SAO, MMB
Mesalia claibornensis . . . . . SAO
Mesalia sp. . . . . MMG
Serpulorbis squamulosus . . . . . SAO
Cheilea sp. . . . . SAO, MMB, MMG, SAJ
Calyptraea aperta . . . . . SAO
Cypraeorbis alabamensis . . . . . SAO
Xenophora sp. . . . . SAO
"Natica" sp. . . . . SAO, MMB
cf. *Sconsia* sp. . . . . GP
Distorsio septemdentata . . . . . SAO
Ficus affinis . . . . . SAO, SAJ
Ficopsis penita . . . . . SAO, MMB
Ficopsis texana . . . . . SAO
Cirsotrema sp. cf.
C.(Coroniscala) spillmani . . . . . MMB
Scalina sp. . . . . GP
Pseudoliva vetusta . . . . . SAO
"Clavilithes abruptus" of Kellum, 1926 . . . . . SAO, MMB
Clavilithes sp. . . . . MMB
Mitra (Fusimitra) sp. . . . . SAJ
Agaronia alabamensis . . . . . SAO, MMB
Voluticella levensis . . . . . SAO
Athleta? cormacki? . . . . . SAO
Caricella pyruloides . . . . . SAO
Caricella spp. . . . . SAO
Santeevoluta wilmingtonensis . . . . . SAO, MMB, MMG
Lyrischapa sp. . . . . MMG
Conus smithvillensis var. . . . . SAO
"Dentalium" sp. . . . . SAO
Eutrephoceras carolinense . . . . . SAO, MMB,MMG, SAJ
Aturia (Brazaturia) sp. cf. *A. laticlavia* . . . . . SAO
Aturia spp. . . . . MMG, GP

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(continued from p. 52)

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BIOSTRATIGRAPHY AND PALEOBIOGEOGRAPHY OF EOCENE COMATULID CRINOIDS FROM FLORIDA

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I. ABSTRACT

Fossil comatulid crinoids are reported herein from two localities and stratigraphic units in Florida. This paper is an interpretation of their paleobiogeographic implications and a description of their biostratigraphic distribution. The crinoid *Himerometra bassleri* Gislén is present in the Lower Ocala Limestone (Eocene) in west central Florida and a second, unidentified species has been found in the Upper Ocala Limestone (Eocene) of northwestern Florida. The specimens of *H. bassleri* represent an addition to the geographic distribution of this genus already known from the Eocene of Louisiana and South Carolina in the Gulf and Atlantic Coastal Plains of the United States. Skeletal elements of *H. bassleri* examined for this study consist of centrodorsals and their associated basal rays and radial plates. The unidentified comatulid specimens from the Upper Ocala Limestone are limited to a single centrodorsal and several brachial plates. *Himerometra bassleri* occurs with other fossils known to have Tethyan affinities, such as the mollusks *Velates* and *Nayadina*. This association, as well as the geographic locations of other fossil and modern species of *Himerometra*, supports an interpretation that the distribution of the crinoids is related to circulation patterns of the Tethys Seaway. A paleobiogeographic shift westward, enabled by the circum-equatorial circulation, resulted in fossil taxa preserved in Atlantic margin areas during the Paleogene; modern taxa, in contrast, have been isolated to the west in the Indo-Pacific region after closure of the Tethys Seaway.

II. INTRODUCTION

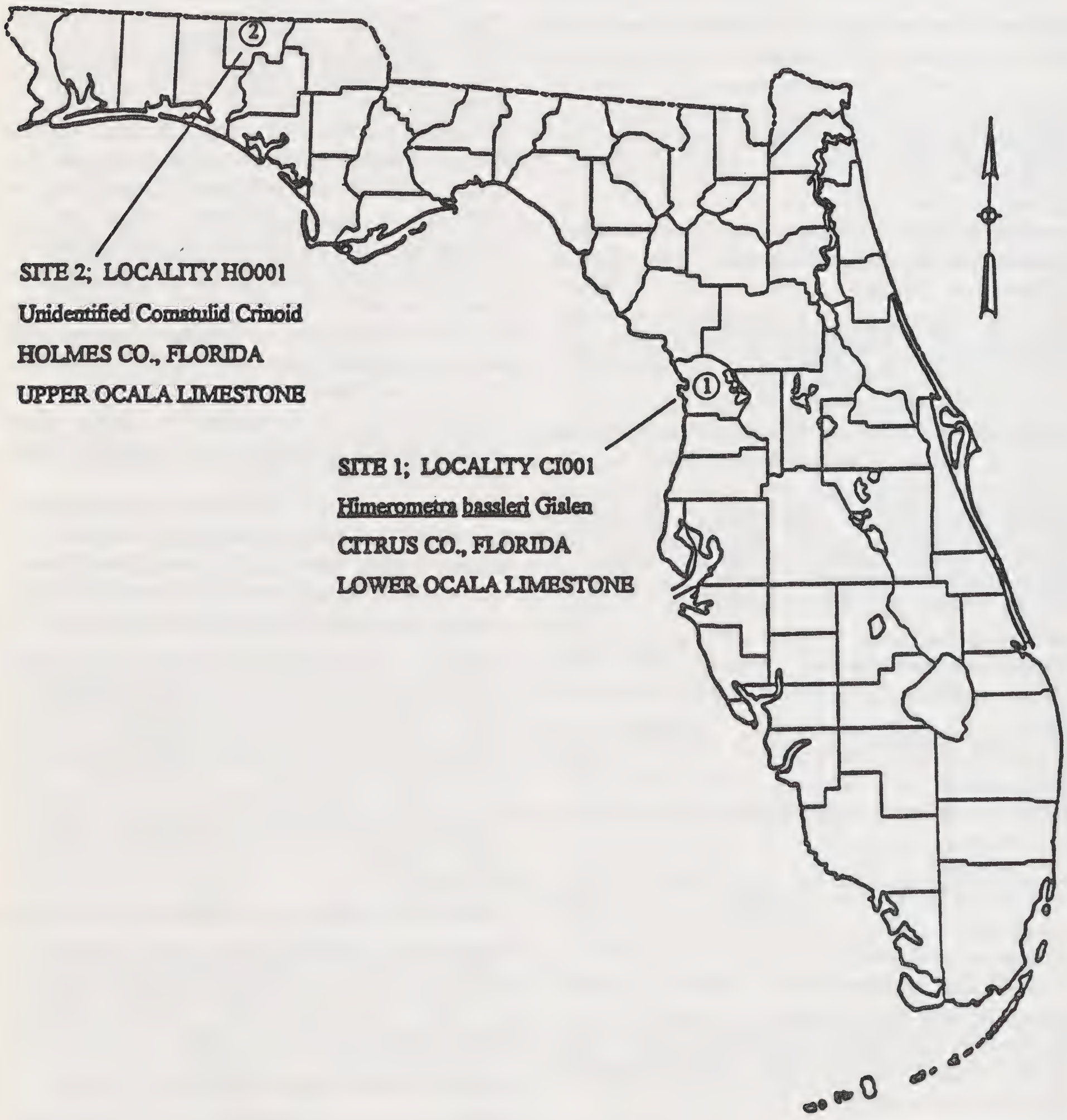
The Cenozoic invertebrate fossil record of Florida consists of both macro- and micro-fossils, which have been studied intensely for more than a century. Echinoderms often have been discussed and described in paleontologic literature regarding Florida. However, most studies have focused on echinoids (*e.g.*, Carter and McKinney, 1992 and references therein), and not the other classes of echinoderms that also have a fossil record. Howe (1942) published a discussion of Tertiary fossils that had been overlooked by Gulf Coast paleontologists, even though the fossils may be abundant. At the time of publication he noted that he was unable to find prior references to four classes of fossil echinoderms, including ophiuroids, comatulid crinoids, asteroids, and holothurians, from these sediments. He attributed the absence of studies on these fossil echinoderms to neglect by paleontologists, not a poor fossil record.

Much work on fossil echinoderms, particularly fossil echinoids, has been completed in the fifty years since Howe wrote his paper. Unfortunately, neglect apparently continues to plague the comatulid crinoids; no detailed discussion of fossil crinoids from Florida has been completed until now. This study describes the occurrence of fossil comatulid crinoids from the Eocene of Florida and discusses paleobiogeographic implications of their distribution in the Coastal Plain of North America with respect to the global distribution of the taxa.

The first report of Eocene comatulid crinoids in North America was by Emmons (1858) regarding fossils from Eocene marls in North Carolina. Gislén (1934) identified and described *Himerometra bassleri* (Plate 1) as part of his remarkable study of over 23,000 disarticulated skeletal ossicles in which he reconstructed and interpreted comatulid arm branching patterns. These ossicles were collected from Eocene (Middle Jacksonian) sediments near Baldock, Barnwell County, South Carolina by R. Bassler as part of an unrelated bryozoan study and then given to Gislén for his

study. Howe (1942) discussed *H. bassleri* with reference to Gislén's (1934) work but did not offer specific taxonomic identifications for comatulid specimens figured in his manuscript. Howe reported comatulid ossicles to be common in Eocene sediments from near Jackson, Alabama, and included at least one figured specimen (Figure 20, *in* Howe, 1942) that may indeed represent an occurrence of *H. bassleri* in Alabama.

Zullo and Kite (1985) reported the presence of *H. bassleri* from the Late Eocene (Jacksonian) Griffins Landing Member of the Dry Branch Formation, Aiken County, South Carolina. This represents a second location in South Carolina from which *H. bassleri* has been collected in addition to the Barnwell County site from which Gislén's original fossil material was collected. Zullo and Kite found fossil comatulid ossicles second in abundance only to barnacles



Text-figure 1. State of Florida map showing known UF localities for comatulid crinoids. Site 1 (UF Locality CI001) represents the collection site for *Himerometra bassleri* Gislén in Citrus County, and site 2 (UF Locality HO001) shows the collection site for the unidentified crinoid in Holmes County.

in their Aiken County samples; thus, both South Carolina localities, as well as Howe's Alabama locality, have been reported to contain significant numbers of comatulid ossicles.

The previous references were the only papers discussing specific stratigraphic distribution of *H. bassleri* until Oyen (1992a, 1992b) reported the occurrence of this species in Florida. Many papers have been published concerning other taxa of modern and fossil comatulids, and several that discuss related taxa will be noted here. Austin Hobart Clark has published a monograph of more than 4300 pages on modern crinoids (Clark 1915, 1921, 1931, 1941, 1947, 1950; Clark and Clark, 1967). This exhaustive study included a taxonomic discussion and description of living species of *Himerometra* (Clark, 1941) that is invaluable for species locations globally. Rasmussen (1978) provided general stratigraphic and geographic information for *Himerometra* and listed the distribution of the Eocene fossils in North America from South Carolina to Louisiana. Unfortunately, Rasmussen did not provide references for locality information; therefore, verification of any reported occurrences other than South Carolina (Gislén, 1934) is not possible. Strimple and Mapes (1984) described two new species of fossil comatulids, *H. caldwellensis* and *H. louisianensis*, from Louisiana. These descriptions were based on a single centrodorsal for each species collected from the Eocene (Jacksonian) Moodys Branch Formation. Rasmussen (1978, p. T890) referred to these Eocene crinoids from Louisiana under the *Heterometra* genus description, not *Himerometra*.

The occurrence of potential comatulid crinoid ossicles in Eocene rocks of Florida was noted by Vernon (1951) but no further identification was given in his paper. His identification seems uncertain given his statement that ". . . small plates believed to be Comatulid brachials are common" (Vernon, 1951, p. 142), in his description of the sediments containing the fossils. This description is for the Eocene (lower Jacksonian) Williston Member of the Moodys Branch Formation in Citrus and Levy Counties, Florida. Vernon also included occurrences of what he calls "brachials" or "comatulid brachials" as part of sediment descriptions from surface outcrops and cores from Orange, Osceola, and Marion Counties in Florida. No plates illustrating these fossils are present in Vernon's paper and the invertebrate paleontology collection of the Florida Geological Survey (now in the Florida Museum of Natural History) does not contain his samples. Therefore, verification of what Vernon was describing as potential comatulid ossicles is not possible. Finally, Oyen (1992a, 1992b) first reported the occurrence of *H. bassleri* in Florida from the Lower Ocala Limestone (formerly Inglis Formation; Jacksonian).

The fossil crinoids examined for this study consist of several different skeletal components from two species of comatulids. Specimens of *H. bassleri* were collected from an outcrop of the Lower Ocala Limestone in northwestern Citrus County, Florida, and another species (not yet identified) of comatulid crinoid was collected from the Upper Ocala Limestone in Holmes County, Florida (Figure 1).

III. ACKNOWLEDGMENTS

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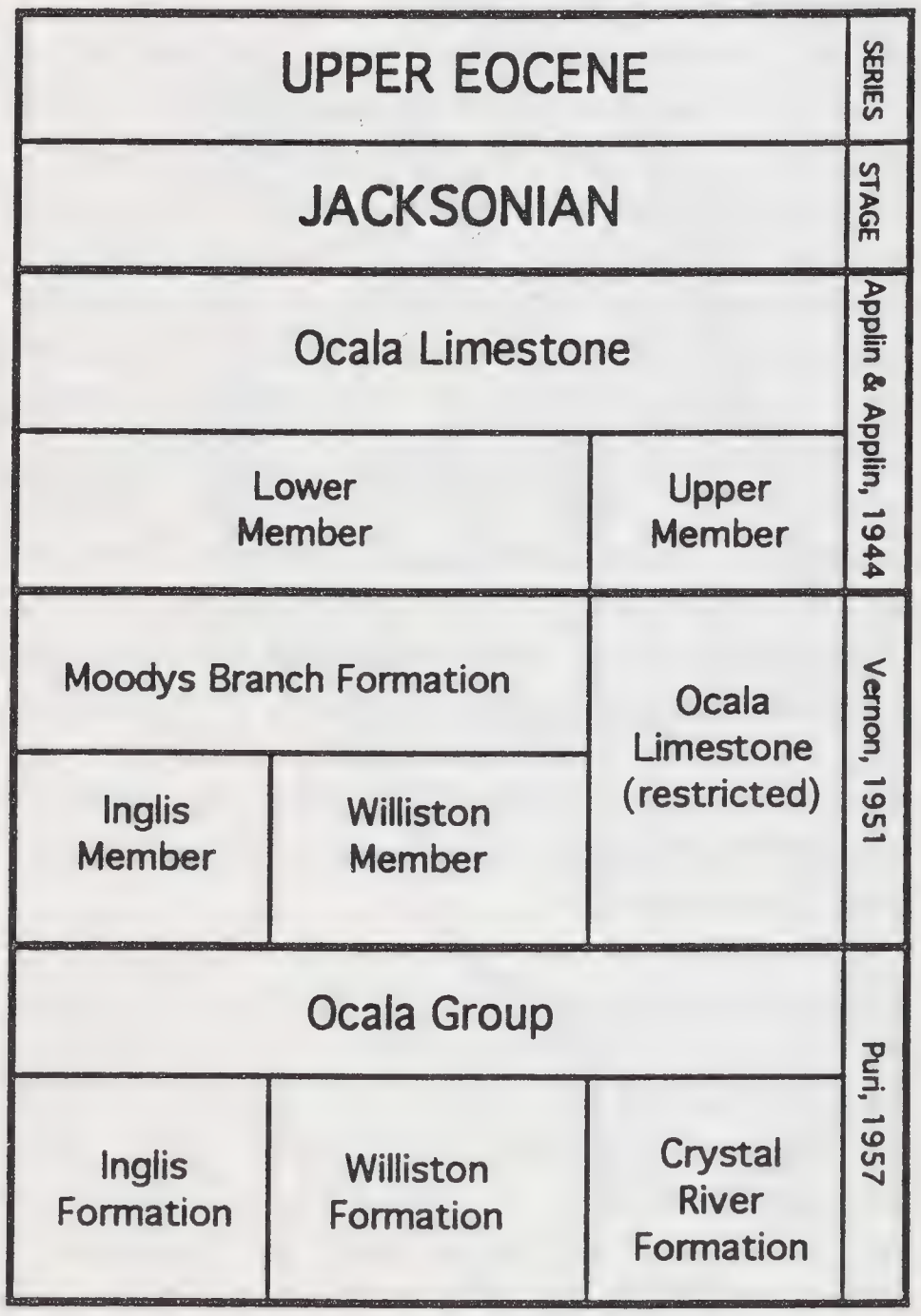
IV. STRATIGRAPHY AND GEOLOGIC SETTING

The stratigraphic nomenclature regarding the Eocene limestones in Florida has yet to be uniformly agreed upon. A brief synopsis of the stratigraphic nomenclature is provided here to illustrate the relationship of terminology used in literature discussing the Late Eocene of Florida. Stratigraphic terminology used in this paper will follow the current usage of Ocala Limestone as a formation unit with the exception of the historical review or when citing previous articles. Previous nomenclature updated to current stratigraphic nomenclature will cite older formation names in parentheses following Ocala Limestone to allow readers unfamiliar with the stratigraphic terminology used in Florida to understand the relationship between units. Problems with the Eocene stratigraphic nomenclature involve determining the stratigraphic status of the Ocala (*i.e.*, should it be a formation or a group?), the status of its subdivisions (*i.e.*, formations or members?), and the relationship of stratigraphic interpretations to the *North American Stratigraphic Code* (North American Commission on Stratigraphic Nomenclature, 1983).

Dall (*in* Dall and Harris, 1892) first used the term "Ocala limestone" for all Jackson age limestones in central Florida. Cooke (1915) continued this formation status, but more importantly, recognized conclusively that the Ocala Limestone was Late Eocene in age because it is found underlying the Marianna Limestone, which is of Oligocene age. Applin and Applin (1944) divided the Ocala Limestone into two units, a Lower and an Upper Member, based on both paleontologic (primarily foraminifera taxa) and lithologic characteristics. Vernon (1951) modified the Applins' nomenclature by elevating their members to formation status, calling the Upper Member the Ocala Limestone (restricted) and the Lower Member the Moodys Branch Formation. Vernon subdivided his Moodys Branch into two members with the upper unit called the Williston Member and the lower unit called the Inglis Member (Figure 2). Puri noted that Vernon used the term "Ocala group" without formally defining the unit and he defined the Ocala Group to include ". . . all calcareous sediments of the Jackson stage in Florida" (Puri, 1957, p. 22). He also re-stated his proposal (1953) to subdivide the Ocala Group into three formations by elevating the members in Vernon's (1951) Moodys Branch to formation status and eliminating the Moodys Branch name. This revision resulted in the Late Eocene Ocala Group being composed of the Inglis Formation, Williston Formation, and a newly defined unit Puri called the Crystal River Formation (in order from lower to upper; see Figure 2). The Crystal River Formation, therefore, is considered synonymous with the "Ocala limestone (restricted)" of Vernon (Puri, 1957, p. 31).

Most workers studying the Late Eocene limestones in Florida since 1957 have followed the stratigraphic nomenclature of either Applin and Applin (1944) or Puri (1957). One of the reasons for the split in



Text-figure 2. Stratigraphic nomenclature comparison diagram for the Upper Eocene in Florida. Note the status of the Ocala as applied by the three authors and the potential for confusion regarding the stratigraphic hierarchy.

acceptance of these stratigraphic interpretations follows the use by the United States Geological Survey (USGS) and the Florida Geological Survey (FGS). The USGS has chosen to follow the Applin and Applin nomenclature and interpretation while the FGS followed Puri's nomenclature in their publications. In 1991, the FGS returned to using the Applin and Applin stratigraphic terminology for the Late Eocene (Scott *et al.*, 1991). A major reason for the disagreement in stratigraphic nomenclature for the Eocene of Florida is the use of fossils to determine formation boundaries, particularly by Puri. He established several faunizones for the Ocala Group and subsequently divided the Ocala into three formations based principally on the faunizones, not lithologic characteristics. This is not in accordance with the definition of a formation as found in Article 24(c) of the *North American Stratigraphic Code* (NACSN, 1983, p. 858). Such use of fossils defines a biostratigraphic unit rather than a lithostratigraphic unit, such as a formation. It should be noted, however, that all of the stratigraphic interpretations presented here for the Eocene were made prior to the establishment of some of the "rule books" for stratigraphic nomenclature including the *Code of Stratigraphic Nomenclature* (ACSN, 1961), the *International Stratigraphic Guide* (ISSC, 1976), and the *North American Stratigraphic Code* (NACSN, 1983).

An additional area of debate among stratigraphers is the age of the Lower Ocala Limestone. Many invertebrate paleontologists still refer to the Lower Ocala as a lower Jackson Stage equivalent, but vertebrate faunas associated with the formation are considered to be upper Middle Eocene (Upper Claibornian Stage) by some vertebrate paleontologists (*e.g.*, Domning *et al.*, 1982). In addition to fossil sirenians, other fossil vertebrates collected from the Lower Ocala Limestone in Citrus County also support a Middle Eocene age determination (Gary Morgan, personal comm., 1993). The stratigraphic position of the Lower Ocala is not critical for this study since Tethyan associated invertebrates are found in Middle Eocene as well as Upper Eocene deposits (see Palmer, 1967). Implications of the stratigraphic and geographic distribution of the comatulids is discussed more thoroughly in the paleobiogeography section of this paper.

Although it is beyond the scope of this discussion to describe in detail the specific problems with the previous stratigraphic interpretations, readers who are not familiar with Florida geology must be aware that recent publications regarding the Upper Eocene may use either system of nomenclature for these Eocene rocks. In this paper, the formation names of Applin and Applin (1944) are used in accordance with the USGS and, more recently, the FGS. More detailed reviews of Eocene stratigraphic nomenclature can be found in most of the previously cited references, as well as in Hunter (1976) and Jones (1982). In addition, Randazzo (1976) illustrates several specific problems with the Florida stratigraphic nomenclature as related to the *North American Stratigraphic Code*.

The geologic setting and depositional environments of the Late Eocene in Florida have been interpreted and discussed by many workers doing paleontologic, stratigraphic, or sedimentologic research. Lithologic descriptions of the Ocala Limestone (or its stratigraphic equivalents) may be found in numerous publications, including several of the previously cited references such as Applin and Applin (1944), Vernon (1951), Puri (1957), Randazzo (1976), and Hunter (1976). The general lithology of the Lower Ocala (Inglis Formation) consists of a light cream to tan colored, chalky, porous, soft to densely crystalline, fossiliferous packstone or grainstone. Randazzo and Saroop (1976, p. 280) reported an average fossil content of 33.7% by volume with up to 60% fossil grains in some facies. Miliolid foraminifera dominate the fossil grain components and significant numbers of additional fossils such as mollusks, crustose algae, ostracodes, echinoids, and bryozoans are preserved, in addition to the forams. Finely crystalline dolomite is present as a limited lithologic component (Chen, 1965), but only minor (usually less than 10%) non-carbonate grains such as quartz are present in the limestones of the Lower Ocala (Inglis Formation). The general lithology of the Upper Ocala Limestone is more variable than the Lower Ocala and is dependent on the facies examined. It is a cream to white

colored, chalky, porous, soft and granular to dense and crystalline, fossiliferous wackestone to grainstone. Fenk (1979) noted a trend toward muddier lithologies in the Upper Eocene, with micrite-rich wackestones and packstones more common than in the Lower Eocene stratigraphic units. The limestone has abundant foraminifera, mollusks, echinoids, bryozoans, ostracodes, and smaller percentages of coralline algae, crustaceans, and corals. Puri (1957) describes portions of the Upper Ocala (Crystal River Formation) as a soft coquina because of the high abundance of fossil material, and the faunal diversity as a whole is greater in the Upper Ocala than in the lower units of the Eocene, including the Lower Ocala (Inglis Formation). Although the lithology is more mud-rich in the Upper Eocene, the volume of non-carbonate grains is still very low, with generally less than 5% insoluble residue present (Oyen, unpublished data).

Late Eocene sediments of the Florida Platform have been interpreted to represent warm, shallow marine environments on a relatively flat, carbonate shelf similar to those found on the modern Great Bahama Bank (Chen, 1965). Several lithofacies (or subfacies) have been identified in the Ocala Limestone, and these facies show changes between high and low energy conditions associated with transgressive and regressive sequences on the Florida Platform. A general transgressive sequence has been interpreted for the limestones found during the time between deposition of the Lower Ocala (Inglis Formation) and deposition of the Upper Ocala (Crystal River Formation) (Fenk, 1979). The Lower Ocala (Inglis Formation) is interpreted to represent higher energy, shallow subtidal environmental conditions that predominated during the Early Jacksonian (Randazzo and Saroop, 1976; Fenk, 1979). Cleanly washed packstone and grainstone lithologies seem to support the higher energy interpretation, since winnowing of carbonate mud has occurred to produce these lithologies. The Upper Ocala (Crystal River Formation) fauna and lithologies of muddy packstones and wackestones are interpreted to represent relatively lower energy, deeper subtidal conditions during the Late Jacksonian (Fenk, 1979). Carbonate mud-rich packstones and wackestones that dominate the lithologies of the Upper Ocala (Crystal River Formation) support this interpretation of deposition in deeper water, below the effective wave base, where intense winnowing occurs.

Cheetham (1963) made paleobathymetric and paleoecologic interpretations for these stratigraphic units using fossil cheilostome bryozoans, and his interpretations are similar to those of Fenk and of Randazzo and Saroop, with only minor differences regarding the water depth during the Early Jacksonian. Cheetham's work is important for understanding the ecologic conditions during the Eocene in the Florida Platform environment. Since cheilostome bryozoans as a group can be considered stenohaline and various species are stenothermal, he concluded that during most of the Eocene the platform was characterized by normal, open marine salinities and temperatures ranging from 19-26° C (Cheetham, 1963, p. 32). Open marine circulation and salinity are important for the paleobiogeographic interpretations of the comatulid crinoids presented below, because echinoderms are also stenohaline organisms requiring open marine salinities. Therefore, the environmental setting in Florida during the Jacksonian

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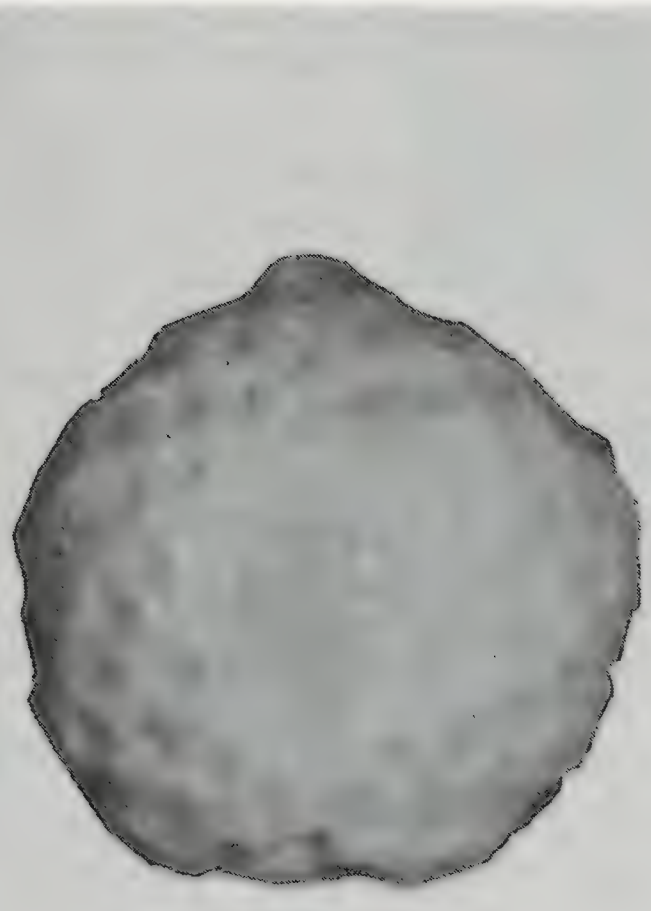
PLATE 1

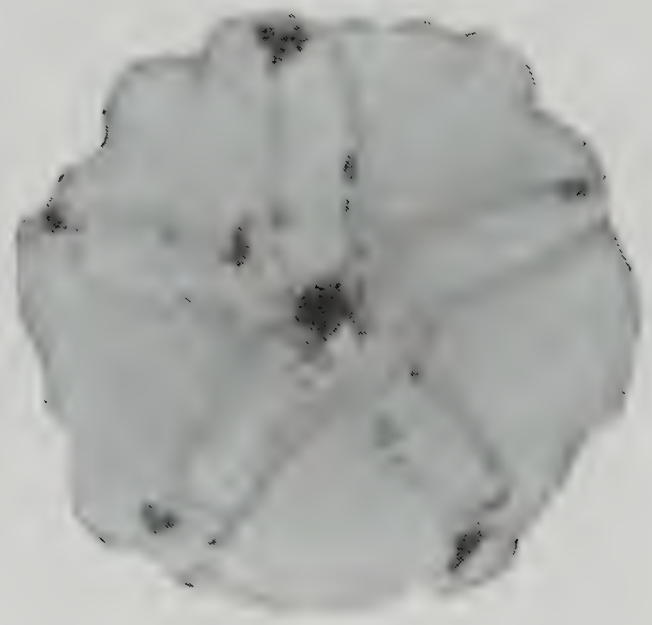
Figures

1. *Himerometra bassleri* Gislén, 1934. Locality: UF C1001.
   1a. UF 39067; dorsal view of centrodorsal element (X5).
   1b. UF 39067; ventral view of centrodorsal, with attached radial plates (X5).
   1c. UF 39088; ventral view of centrodorsal, with radial plates absent, which allows distinctive rod-shaped basal rays to be observed (X5).
2. Unidentified comatulid crinoid. Locality: UFG HO001.2a. 126; dorsal view of centrodorsal element; diameter 2.0 mm (X10).
   2b. UF 48126; ventral view of centrodorsal element; diameter 2.0 mm (X10).
   2c,d. UF 48125; brachial plates; lengths approximately 1.5 mm (X10)



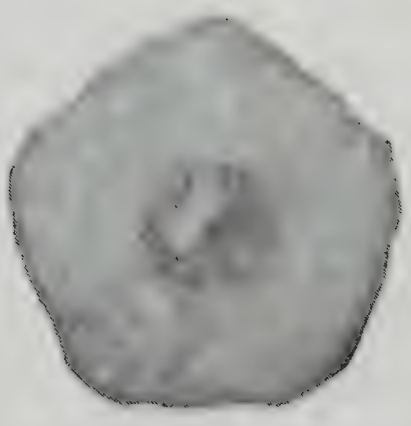
1a

1b



1c

2a



2b

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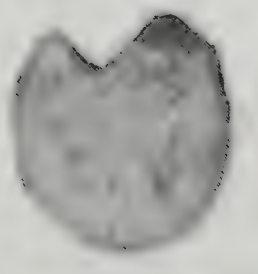


2d

PLATE 1

was suitable for inhabitation by the crinoids, and analogous to that which exists in the Bahamas Bank today.

V. MATERIALS STUDIED

Fossil crinoid specimens discussed in this study were collected from two localities in Florida (Figure 1). These fossils are disarticulated skeletal ossicles from two species of comatulid crinoids, *Himerometra bassleri* Gislén and a second, as yet unidentified species. Specimens of *H. bassleri* were collected in 1974 by FLMNH researchers during bulk sampling of Early Pleistocene sediments (which contained weathered out remains of thousands of Lower Ocala Limestone invertebrates from surrounding limestones) for fossil vertebrate material. Upon sieving, the comatulid fossils were separated from matrix material and placed, unidentified, in the Invertebrate Paleontology Collection of the museum. (This example seems to correlate well with Howe's [1942] belief that comatulids are probably more common in Coastal Plain strata than previously known simply because they were neglected by researchers, whether intentionally or unintentionally.) The collection of *H. bassleri* consists of skeletal components including 50 centrodorsals, 53 radial plates, and 20 basal rays found at UF locality CI001 (UF 39054 - UF 39090). Specimens are small, with most centrodorsals less than 10 mm in diameter, and the effects of sedimentary diagenesis (including recrystallized ossicles and epitaxial cements) are visible in many of the fossils. Plate 1 shows representative views of the dorsal and ventral surfaces of the centrodorsal, included radial plates, and basal rays for this species, as well as the imperfect preservation state of the crinoid components.

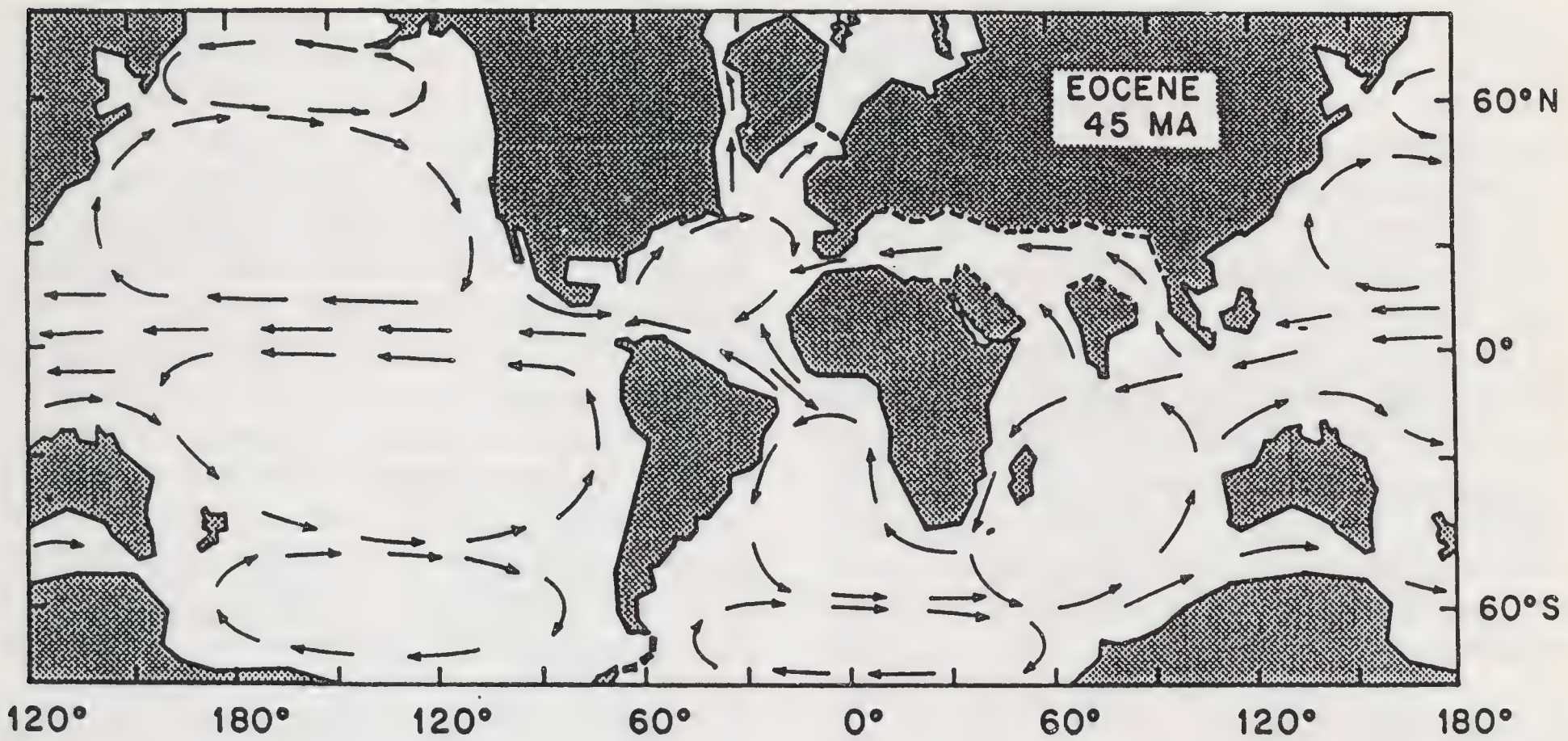
A second species of comatulid crinoid was discovered in 1992 while picking through the fine-fraction matrix of a bulk sample collected in 1977 from the Upper Ocala Limestone (Crystal River Formation). The number of skeletal components found consists of five brachial plates and only one centrodorsal from UF locality HO001 (UF 48125 and UF 48126). Plate 1 shows dorsal and ventral views of the centrodorsal and two of the five brachial plates. These specimens are distinctly smaller than those of *H. bassleri*, with the centrodorsal measuring approximately 2.0 mm in diameter and the brachials averaging 1.0-1.5 mm in length. The taxonomic status of these specimens is still uncertain and more work is currently being done to determine which species of comatulid crinoid is present in the Upper Ocala Limestone (Crystal River Formation) of Florida.

VI. PALEOBIOGEOGRAPHIC CONSIDERATIONS

Examination of the paleobiogeographic and stratigraphic distribution for species of *Himerometra* shows an interesting pattern during the geologic history of the genus. Ten species of *Himerometra* have been described in the literature, with six extant species and four fossil species from the Eocene (three species) and Oligocene (one species). In order to understand better how the biogeographic distribution pattern for this genus may have been produced, we must consider the life histories of these crinoids.

Three general patterns of development exist for marine invertebrate organisms (Barnes, 1980). These include: 1) direct development – having no larval stage; 2) planktotrophic development – having feeding larvae with a relatively long larval life; and 3) lecithotrophic development – having non-feeding larvae dependent on nutrition from yolk sacs during their relatively short larval life. Larvae also may vary between active, free-swimming varieties or passive, non-swimming forms. The phylum Echinodermata is diverse and development styles are consistent only at lower taxonomic levels. Modern crinoids are the only living class of echinoderm in which the entire larval development stage is lecithotrophic and which, therefore, lack the ability to feed (McEdward *et al.*, 1988). A consequence of a lecithotrophic larval stage is its reduced larval stage duration as compared to typical planktotrophic larval stage durations; the larval dispersal range is limited by a finite energy source available in its yolk.

The relationship between larval dispersal ability and paleobiogeographic distribution for the species of *Himerometra* is yet uncertain because of limited data regarding specific larval stage duration for these taxa. Breimer (1978, p. T53) pro-



Text-figure 3. Inferred global surface circulation patterns during the Middle Eocene. The circum-equatorial Tethys Seaway would provide a path for global distribution of species of *Himerometra* as noted in the fossil record from sites in the southeastern United States, Germany, and modern faunas in the Indian-Pacific Oceans regions (figure from Haq, 1981).

vided a general time range of 5 to 108 hours for the swimming larval stage of modern crinoids. McEdward *et al.* (1988) assembled development times for ten species of modern crinoids, including at least one genus (*Heterometra*) in the family Himerometridae. The development times range from one to six days (see McEdward *et al.*, Table I, for details) for those species for which data are available. The key point to note is that all larval stage durations listed are relatively short (less than six days) and the dispersal range achieved in the larval stage only is likely to be small. This presents a problem for reconstructing the dispersal methods that have allowed the paleobiogeographic distribution for *Himerometra* species to become established as known from the fossil record. Further, the stratigraphic occurrences of these species are apparently anomalous since fossil species are known from the Eocene and Oligocene, and Recent species are found in the Indian and Pacific Oceans, but no fossil reports are known from the Miocene through the Pleistocene.

A common link among the geographic occurrences of the fossil and modern species is their location in an approximate circum-equatorial belt that generally corresponds to the position of the Tethys Seaway (Figure 3). Eocene species *H. caldwellensis*, *H. louisianensis*, and *H. bassleri* are found in the Coastal Plain of the southeastern United States, and the Oligocene species *H. grippae* is found in Europe (Germany). The six modern species (*H. bartochi*, *H. magnipinna*, *H. martensi*, *H. persica*, *H. robustipinna*, and *H. sol*) are distributed in the southwestern Pacific Ocean to the Indian Ocean, with one of the species also known from the Persian Gulf (Clark, 1941). Dispersal of the crinoids may have been aided by the ocean currents of the Tethys Seaway during both the larval and adult stages of their lifespan. The *H. bassleri* specimens from Florida can be considered part of the Tethyan fauna due to their stratigraphic and faunal relationship with previously established Tethyan faunal assemblages. Mollusks are the dominant Tethyan faunal members associated with the crinoids found in the Lower Ocala Limestone. Descriptions of these mollusks and their stratigraphic distribution include papers by Richards and Palmer (1953), Palmer (1967), Givens (1989), and Nicol (1991), among others. The association of *H. bassleri* with the Tethyan mollusks leaves little question that the comatulids in Florida were influenced by circulation of the Tethys Seaway, and this

allows an inference that other fossil and modern *Himerometra* occurrences may also have resulted (at least to some degree) from this circulation influence.

Several lines of reasoning support the idea that the Tethys Seaway contributed to the crinoids' distribution, but was not the only factor involved. First, the rate of flow of currents in the Tethys probably was not fast enough to transport the larval crinoids across an ocean basin within a single larval stage prior to metamorphosis. Scheltema (1977) discussed larval dispersal techniques and their relationship to the Tethys Seaway and provided calculated flow rates as well as travel time during the Late Cretaceous. The equatorial Tethys current had a velocity of 2-4 knots at this time, and taking into account the size of the Late Cretaceous Atlantic Ocean, it is estimated the passive travel time across the Atlantic was 28-56 days. Assuming a similar current velocity for the Eocene and Oligocene, the travel time would be significantly longer due to the continual tectonic spreading along the Mid-Atlantic Ridge system, resulting in a greater distance to travel in periods younger than the Cretaceous.

Using information regarding larval stage durations discussed earlier (all less than seven days), it is unlikely that transport across the entire ocean basin occurred within a single lifespan of these comatulids, if we assume transport is limited to the larval stage only. Current knowledge regarding crinoid development rates and styles of development (lecithotrophic *versus* planktotrophic) however, is quite limited, and information regarding fossil crinoids is unknown or uncertain, so the possibility exists that different development rates or styles existed earlier in the evolutionary history of crinoids, which may have allowed greater dispersal distances to occur through several different methods than presently known from modern crinoids (Larry McEdward, personal comm., 1992).

A second problem exists in defining the Tethys as the primary paleobiogeographic control over the distribution of *Himerometra* species. This is due to the poor biostratigraphic record of the genus and its geographic distribution with respect to the Tethys Seaway. The genus evolved in the Eocene, according to the known stratigraphic record, and three species are known from the southeastern Gulf and Atlantic Coastal Plains of the United States. The sole reported species in the Oligocene is found in Germany. If the Oligocene species did not evolve independently, then it is less likely the Tethys provided the contact, and more likely the Gulf Stream was responsible (see Figure 3). Again, a transport problem exists based on larval stage durations if trans-Atlantic transport was required. Alternatively, Tethyan transport could have occurred westward from North America to Europe, but stepwise transport (*i.e.*, establishment of numerous successive populations) may have been required for this to happen (see Scheltema, 1977). Unfortunately, the stratigraphic record for *Himerometra* species is very limited and they are known only from the United States and Germany. The geographic ranges on modern *Himerometra* species in the Indo-Pacific region, however, would support this idea; no species are known in the fossil record from the Miocene through the Pleistocene.

Perhaps the most difficult aspect of interpreting paleobiogeographic and evolutionary patterns of the genus *Himerometra* is the poor fossil record. This is a problem common to most fossil taxa, but it seems to be somewhat more pronounced in the comatulid crinoids (as the paucity of references on these fossils would support) than in other taxonomic groups. As Howe (1942) noted, this is likely due to neglect and lack of recognition of skeletal fragments by paleontologists rather than rarity of fossil materials. The preservation potential for these crinoids is good (at least for individual skeletal plates) because of their high-Mg calcite composition. Furthermore, the comatulid skeleton normally disarticulates quickly and individual plates are quite small and may be overlooked in the field. Finally, comatulid crinoids seem to be poorly recognized by many workers and likely overlooked unintentionally even when present in the strata. It is hoped that this report will help bring attention to fossil comatulids and aid other paleontologists in recognizing these fossils when examining samples and outcrops. As work continues on fossil comatulids such as *Himerometra*, our ability to refine what is known about the biostratigraphic and paleobiogeo-

graphic distribution of these fossils will only improve.

VII. LOCALITY DATA

The following are collecting localities of the Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida (UF):

CI001 Late Eocene (Jacksonian), Lower Ocala Limestone (Inglis Formation), outcrop located on north bank of Cross Florida Barge Canal, vertebrate site Inglis 1A, (SE 1/4, SE 1/4, sec. 9, T17S, R16E, Yankeetown 7.5' USGS quadrangle), Citrus County, Florida.

HO001 Late Eocene (Jacksonian), Upper Ocala Limestone (Crystal River Formation), natural outcrop in a spring run on Wright's Creek, approximately 4-5 mi (6.4-8.1 km) north of Bonifay, (SW1/4, SE1/4, sec. 2, T5N, R15W, Bonifay 7.5' USGS quadrangle), Holmes County, Florida.

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MOLLUSCS OF THE NATURAL WELL LOCALITY, DUPLIN STRATOTYPE, NEAR MAGNOLIA, NORTH CAROLINA, AND REDISCOVERY OF *CARINORBIS QUADRICOSTATA* (EMMONS, 1858) (GASTROPODA: AMATHINIDAE)

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I. ABSTRACT

The Duplin Formation stratotype at the Natural Well limestone sink near Magnolia, North Carolina, is commonly thought to be the source of one of the most thoroughly documented Pliocene molluscan faunas in the Carolinas. However, few of the 196 species listed by Dall (1903) as from "the Duplin well or the adjacent village of Magnolia" were actually collected from Natural Well. Neither the coding of Dall's lists nor reference in text clearly indicates which specimens were collected from the stratotype section.

A stratigraphically pure Natural Well collection, housed in the Geology Department of the University of North Carolina at Chapel Hill, contains 239 molluscan species (Appendix I). The faunule is low in endemics and high in first appearances of species that continue into the younger Waccamaw faunas. Like the correlative Tearcoat Branch and Muldrow Place faunules, the Natural Well faunule contains only a single pectinid species, the ubiquitous *Carolinapecten eboreus*.

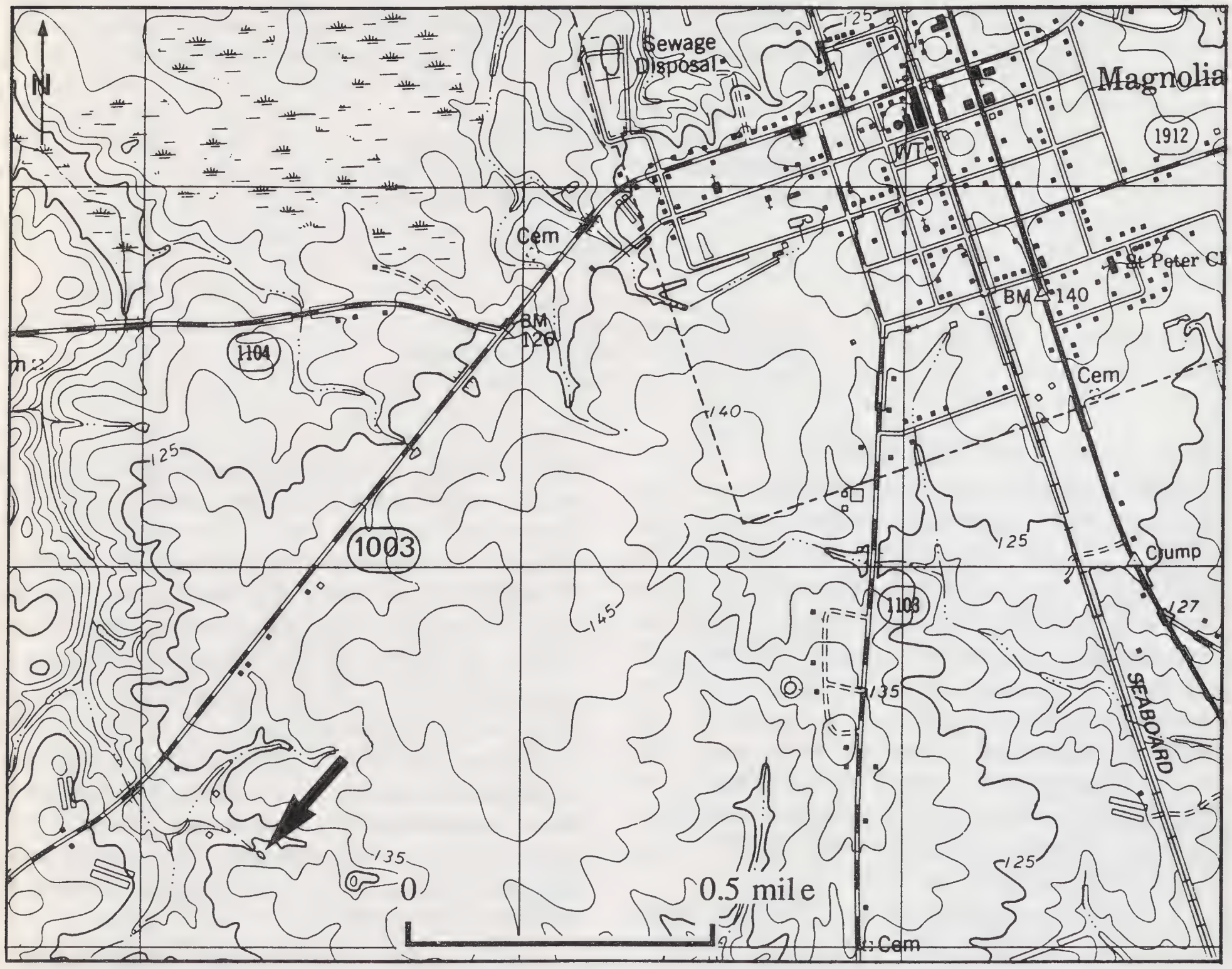
The UNC-CH collections contain a number of rare and unusual species, including a single specimen of *Carinorbis quadricostata* (Emmons, 1858). This is only the third recorded specimen of this rare and endemic species, and the first that permits comparative systematic analysis. The genus *Carinorbis* has been overlooked or inaccurately synonymized in most literature.

II. INTRODUCTION

The Duplin beds have had a varied history of stratigraphic assignments. Originally defined (Dall and Harris, 1892) in terms of the Hodge (1842) section at Natural Well near Magnolia, North Carolina, the Duplin Formation contained both a sandy shell "marl" stratum and an underlying argillaceous bed. Cooke (1945) expanded the formational concept to include "late Miocene" (now Lower and mid-Pliocene) deposits extending from the Neuse River to northern and western Florida. Huddle (1940, p. 227) reported a section of "5-10' of Pleistocene sand, 3-4' of shell marl and about 14' of light green calcareous and argillaceous sand with interbedded calcareous sandstones." However, Huddle reported Eocene microfossils from the green, argillaceous sand, leaving only 3 to 4 feet of Duplin stratotype.

Berry (1947) included the Duplin within an expanded concept of the Yorktown Formation. Ward *et al.* (1979) abandoned the term "Duplin Formation" in favor of a similarly expanded Yorktown concept, but Bailey (1987) and Ward, Bailey, and Carter (1991) have resurrected the Duplin.

The discovery of at least three transgressive-regressive pulses, each with related but distinctive faunas, in the "Duplin" of South Carolina (M. Campbell, 1992) prompted a reexamination of the reported fauna at Natural Well. Dall (1903, p. 1599-1603) listed approximately 300 species of "Duplin" molluscs, but Dall's list was a composite from several localities and literature citations, including 196 species "authentically collected at the Duplin well or the adjacent village of Magnolia by Burns." The composite nature of this list was soon overlooked in subsequent literature. Clark *et al.* (1912, p. 241) observed: "Many lists of fossils obtained at the Natural Well have been published at various times. The most complete one is that given by W. H. Dall in vol. III of the Transactions of the Wagner Free Institute of Science."



Text-figure 1. Location of Natural Well, near Magnolia, North Carolina. Warsaw South 7.5 minute quadrangle. Figure after Carter *et al.*, 1988.

Dall's Duplin list contained *Terebraspira elegans* (Emmons), *Barbatia centenaria* (Say), and *Mercenaria tridacnoides* (Lamarck). He records several pectinids from "Natural Well and Magnolia," including *Chesapecten septenarius* and *Amusium mortoni*. *Chesapecten edgecombensis* (= *C. madisonius*) was cited as Duplin, but without specific locality.

These species have not been recovered subsequently from Natural Well or equivalent beds, but are characteristic of the older Goose Creek Limestone and Raysor faunas in South Carolina. In southern Florida, *Chesapecten septenarius* and *C. madisonius* (low rib number form) are restricted to the Tamiami Limestone, a pre-Pinecrest (*i.e.*, pre-Duplin) unit, and *Mercenaria tridacnoides* is found only in the Tamiami and the basal Pinecrest. In the Virginia Yorktown Zone 2 faunas, *Chesapecten madisonius* (10-16 rib form) is restricted to the basal beds, and *Barbatia centenaria*, *Mercenaria tridacnoides*, and *Chesapecten septenarius* are present only in the lower and middle (pre-Duplin equivalent) Zone 2 beds (L. Campbell, 1993). Typical *Chesapecten madisonius* (16-26 rib form) is found throughout the middle and upper beds of Zone 2 (L. Campbell, 1993). Consequently, both Dall's general "Duplin" list and the specific records in text appear to represent a stratigraphically composite assemblage.

Dall and Harris (1892, p. 72-73) observed of Natural Well:

> "This locality has recently been visited by Mr. Frank Burns, of the U. S. Geological Survey, who reports the 'well' or sink to be situated in the midst of a hard-wood 'hammock' covering a few acres.... Much of the marl has been removed for use as a fertilizer and good speci-

> mens of fossils are now rare. But better exposures of the marl can be found in the immediate neighborhood of Magnolia, a village about 2 miles northeast from the well. On the farm of Mr. Strickland, 1 1/2 miles northwest from Magnolia, the same bed afforded better preserved fossils than at the well, while on the farm of Mr. Hollingsworth, 2 miles northeast of Magnolia, the marl is cemented into a comparatively solid rock, hard enough to burn for lime."

In other words, few if any of the Burns collection specimens recorded from Natural Well and the vicinity of Magnolia and cited by Dall (1890-1903), Mansfield (1930, 1932) and Gardner (1944, 1948) actually came from Natural Well. Apparently, the Strickland farm is the source of most of Burns' "Natural Well" specimens, but the Hollingsworth farm cemented marl "hard enough to burn for lime" suggests Goose Creek Limestone lithologies, which would provide a credible source for the *Chesapecten* species and other anomalous "Natural Well" pectinids. An abbreviated assemblage from the Strickland farm is preserved in the U. S. Geological Survey stratigraphic collections at the National Museum in Washington, D.C. Hodge (1842, p. 335-336) stated that "the shells [at Natural Well] are of a great variety of species belonging to this formation, and they lie promiscuously together in great confusion." One hundred and fifty years later, the Natural Well faunule continues to lie in a state of unsuspected confusion.

From the 1890's to the early 1950's, access to the Duplin sands at Natural Well was limited by the precipitous nature of the exposure and the undercutting produced from mining the Duplin layer for agricultural lime. In the early 1950's, Charles Locklin had a ramp cut to facilitate collecting (Druid Wilson, 1990, personal communication). The Caloosahatchee and Pinecrest portions of the Locklin collection went to the Academy of Natural Sciences of Philadelphia (Olsson and Harbison, 1953), but we have not located the Locklin Natural Well collection.

An independent and stratigraphically pure collection of Natural Well fossils at the University of North Carolina at Chapel Hill, assembled by John W. Frink, Walter Wheeler, Joseph G. Carter, and their students over the past sixty years, permits a reexamination of the stratotype Duplin biota. Two hundred and thirty-nine molluscan species can be documented in literature or in the Chapel Hill collection (Appendix I). Preliminary comparisons indicate a strong correlation with the faunule at Tearcoat Branch, Sumter County, South Carolina (S. Campbell, 1974), and with the *Cancellaria* zone fauna of western Florida (Mansfield, 1930, 1932). The nannofossil age of the Natural Well stratotype was given by Cronin *et al.* (1984) as NN 16-18.

We concur with Bailey (1987) that the term "Duplin" should be reinstated, but we suggest that the lithostratigraphic concept should be narrowly restricted to the Natural Well stratotype and lithologically equivalent beds. Owens (1991) mapped the area from Cape Fear to Georgetown, South Carolina, using an expanded concept of the Duplin Formation, while Weems and Lemon (1988) mapped quadrangles in the Charleston area, using a more restricted concept.

Using a narrow lithostratigraphic interpretation of the Natural Well stratotype, the Duplin includes: (1) the Natural Well section; (2) the Strickland Farm; (3) Bed E at the Robeson Farm near Tar Heel, North Carolina (Britt *et al.*, 1992); (4) Tearcoat Branch and Muldrow Place, Sumter County, South Carolina (S. Campbell, 1974); and (5) Kirby's Pond, Timmonsville, Florence County, South Carolina. A total of 453 molluscan species can be documented from these sites. A biostratigraphic statistical summary of the Natural Well faunule is given in Table 1.

The Natural Well faunule includes many tropical and sub-tropical elements. The Duplin fauna, typified by the Natural Well faunule, is low in endemics, being a major transitional fauna in both space and time. Spatially, the subtropical Duplin borrows heavily from the tropical Pinecrest faunas of southern Florida and from the rich, warm temperate faunas of the Yorktown in Virginia and northern North Carolina. Lateral biofacies are admixed at Natural Well, Tearcoat Branch, Muldrow Place, and Timmonsville, each locality blending taxa typical of modern littoral, sublittoral, shallow, mid-, and outer shelf biotopes. Despite the resulting diversity, the Natural Well fauna has yielded only a single pectinid species, the ubiquitous *Carolinapec-*

TABLE 1
STATISTICAL SUMMARY OF DUPLIN MOLLUSCAN SIMILARITY LEVELS

	R	UW	LW	E	D	RA	UGC	LGC	M
%	18.8	46.0	46.0	64.5	95.8	45.6	38.5	24.3	18.0
Dice	.179	.383	.341	.155	.662	.487	.441	.324	.248

% = Percentage in Common
Dice = Dice Similarity Index (2 x C) / (A + B)
C = species in common, A = species in assemblage A, B = species in assemblage B

R = also Recent; UW = Upper Waccamaw; LW = Lower Waccamaw;
E = beds at Elizabethtown; D = Duplin; RA = Raysor; UGC = Upper Goose Creek Limestone; LGC = Lower Goose Creek Limestone;
M = also Miocene. (For more detailed stratigraphy, see M. Campbell and L. Campbell, this volume).

Note: The Natural Well faunule does not completely equate with the Duplin standard because a small number of taxa from Natural Well were not identified to species.

ten eboreus. The older, less diverse Raysor and Goose Creek faunas have higher rates of endemism and include several pectinid species.

As a time-transitional fauna, the Duplin combines many last-appearance records from the older Raysor and Goose Creek faunas with numerous first-appearances of species continuing into the younger Waccamaw faunas.

The University of North Carolina Natural Well collection contains a number of unusual species, including a single specimen of *Carinorbis quadricostata* (Emmons, 1858), a species which has not been recognized subsequent to its initial discovery. This discovery prompted a review of the genus *Carinorbis* Conrad, 1862, and the two Duplin species in this genus.

III. SYSTEMATIC PALEONTOLOGY

Class GASTROPODA
Superfamily PYRAMIDELLOIDEA
Family AMATHINIDAE Ponder, 1987
Genus CARINORBIS Conrad, 1862

Carinorbis CONRAD, 1862, Acad. Nat. Sci. Phila., Proc., v. 14, p. 288.

Type species: *Delphinula lyra* Conrad, 1834, here designated.

Original Description: "Suborbicular; spire small, depressed, or but little prominent; shell costate, ribs revolving, distant, prominent; last whorl flattened above; umbilicus small, and the space beneath it channeled; peristome continuous." (Conrad, 1862, p. 288)

Discussion: Conrad (1862) originally assigned two species to *Carinorbis: Delphinula lyra* Conrad, 1834, and *Delphinula quadricostata* Emmons, 1858. No type species was originally or subsequently designated. Conrad (1863, p. 570) then muddled the concept of *Carinorbis* by assigning to it four additional species, a trochid and three very different vitrinellids, none of which are congeneric with *Delphinula lyra* and *Delphinula quadricostata*.

Carinorbis lyra is the first named of Conrad's (1862) cited species, and it is common in some Yorktown faunules. In contrast, *Carinorbis quadricostata* (Emmons) is known from only three specimens including the missing holotype, and is found only at Natural Well. We, therefore, designate *Delphinula lyra* Conrad, 1834 (probable syntypes ANSP 30731) as type of *Carinorbis* Conrad (1862), although the choice does not affect the nature of the genus since the two taxa are congeneric. Dall (1892) synonymized *Carinorbis* with *Fossarus*. However, like many other taxa traditionally placed in or near *Fossarus, D. lyra* belongs elsewhere (James McLean, 1988, personal communication). *Carinorbis* Yen (1946), and *Carinorbis* Mandahl-Barth (1954) are homonyms (*fide* Vaught, 1989).

Carinorbis lyra is congeneric with *Clathrella clathrata* (Philippi, 1844), Pliocene of Italy, as illustrated by Cavallo and Repetto (1992, sp. 433, here reproduced as plate 1, figure 9), and with *Clathrella costata* (Brocchi, 1814), Neogene and Recent of Europe, as figured by Ponder (1987). Consequently, *Carinorbis* Conrad (1862) is a senior synonym of *Clathrella* Recluz, 1864 [type species: *Clathrella clathrata* (Philippi)]. Although *Clathrella* was synonymized with *Phasianema* by Wenz (1940), Ponder (1987) has shown them to be distinct. *Phasianema* Wood, 1842 (type species *P. sulcata* Wood, 1842 = *Turbo costulata* Brocchi, 1814) is not congeneric with *Carinorbis* and is morphologically closer to *Iselica*. In a footnote, Cavallo and Repetto (1992, p. 154) synomymized *Clathrella clathrata* with *Phasianema costata* (Brocchi, 1814). Their use of *Phasianema* for *Clathrella costata* is not explained. It may follow the usage of Wenz, or could have easily resulted from the confounding of Brocchi's two very similar species names.

Ponder (1987) erected a new family, the Amathinidae, (superfamily Pyramidelloidea), in which he included seven genera, among them *Clathrella*, *Phasianema*, and *Iselica*. Like *Carinorbis*, *Iselica* had previously been assigned to the Fossaridae by most authors.

CARINORBIS LYRA (Conrad)
Plate 1, figures 5-8

Delphinula lyra CONRAD, 1834, Acad. Nat. Sci. Phila., Jour., v. 7, p. 141; CONRAD, 1846, Acad. Nat. Sci. Phila., Proc., v. 3, p. 20, pl. 1, fig. 27.

Delphinula globulus H.C. LEA, 1843, Abstract of a paper read before the American Philosophical Society, (privately printed) p. 9; H.C. LEA, 1845, Amer. Philos. Soc., Trans., preprint, ser. 2, v. 9, p. 36, pl. 36, fig. 74.

Carinorbis lyra CONRAD, 1862, Acad. Nat. Sci. Phila., Proc., v. 14, p. 288; CONRAD, 1863, Acad. Nat. Sci. Phila., Proc. v. 14, p. 570; MEEK, 1864, Smithsonian Misc. Coll., v. 7, no. 183, p. 14; L. CAMPBELL, 1993, Virginia Div. Min. Resources, Publ. 127, p. 69, pl. 30, fig. 331.

Fossarus lyra (Conrad). DALL, 1892, Wagner Free Inst. Sci., Trans., v. 3, pt. 2, p. 322, 347, pl. 18, fig. 3a; CAMPBELL *et al.*, 1975, South Carolina Geol. Notes, v. 19, p. 105, species 907; WARD and GILINSKY, 1993, Virginia Mus. Nat. Hist., Mem. 3, part A, p. 17.

Original Description: "Shell transversely subovate; spire depressed; body whorl with about eight distant very elevated ribs, composed of double laminae; space between the ribs transversely striated; umbilicus small, placed nearer the summit than the base of the shell; aperture dilated; longitudinally suboval. Length, less than half an inch. Locality. Suffolk, Va." (Conrad, 1834, p. 141)

Discussion: *Carinorbis lyra* (Conrad) was illustrated poorly but recognizably by Conrad (1846, pl. 1, fig. 27). The species was more definitively illustrated by Dall (1892, pl. 18, fig. 3a; here reproduced as plate 1, figure 8.) in a figure which inexplicably added an extra rib. The species has five strong and two weaker spiral cords, and about 24 strong, narrow, axial ribs on the adult body whorl, producing a coarsely cancellate sculpture. The shell changes shape with growth, becoming relatively broader because of rapid inflation of the adult body whorl. Adult shells are never common, but immature shells are common in some Yorktown deposits. Specimens are scarce in the Duplin Formation at Natural Well and Tearcoat Branch and rare in the Raysor sands at the Berkeley County Quarry near Cross, South Carolina. Conspecific specimens with high, but thinner, spiral ribs can be found in the Pinecrest beds (bed 8) at the APAC pit, Sarasota, Florida (USGS collections).

CARINORBIS QUADRICOSTATA (Emmons)
Plate 1, figures 1-4

Delphinula quadricostata EMMONS, 1858, Report of the Geol. Surv. of North Carolina, p. 272, fig. 180; DALL, 1892, Wagner Free Inst. Sci., Trans., v. 3, pt. 2, p. 322 (as a synonym of *Fossarus lyra*).

Carinorbis quadricostata (Emmons). CONRAD, 1862, Acad. Nat. Sci. Phila., Proc., v. 14, p. 288; CONRAD, 1863, Acad. Nat. Sci. Phila., Proc., v. 14, p. 570.

Aorotrema gardnerae OLSSON and HARBISON, 1953, Acad. Nat. Sci. Phila., Mon. 8, p. 424, pl. 39, fig. 13; CAMPBELL *et al.*, 1975, South Carolina Geol. Notes, v. 19, p. 99, species 708.

Original Description: "Shell small, thin; whirls [*sic*] few, angulated and furnished with four ribs, which are crossed by lines of growth; aperture angular.

"Found occupying the interior of the large univalve shells of the miocene [*sic*]." (Emmons, 1858, p. 272)

Discussion: Delphinula quadricostata is missing from among the Emmons types at the Paleontological Research Institution, Ithaca, New York. Both Emmons' original figure and the illustration of *Aorotrema gardnerae* of Olsson and Harbison lack the detail necessary for defining *C. quadricostata* as distinct from the more coarsely sculptured *C. lyra*. The presence of a definitive specimen in the University of North Carolina at Chapel Hill Natural Well collections allows recognition of *C. quadricostata* as a distinct species. *Carinorbis quadricostata* differs from *C. lyra* in having four rather than five major spiral cords on the body whorl, in having narrower and lower primary and secondary spiral cords, and in having axial sculpture much reduced, consisting of about 30 very low, narrow riblets on the body whorl. The sculpture is not cancellate as in *C. lyra*. The three known specimens of *C. quadricostata* are much smaller than adult *C. lyra*, and may be immature. Based on Olsson and Harbison's (1953) figure of the type, we judge *Aorotrema gardnerae* to be a minute juvenile of *C. quadricostata*. Emmons' type locality for *C. quadricostata* is unstated, but could have been Natural Well. *Carinorbis quadricostata* appears to be rare, local in its distribution, and easily overlooked due to its small size.

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PLATE 1

Carinorbis species from Virginia, North Carolina, and Italy.

Figures

1-4. *Carinorbis quadricostata*, 4 mm, UNC-15152, Natural Well, near Magnolia, North Carolina.
   1. Adapertural view showing reduced axial sculpture and four prominent keels.
   2. Apertural view.
   3, 4. Apical view showing reduced sculpture and heterostrophic protoconch.

5, 7. *Carinorbis lyra*, 5.9 mm, UNC-15230, Rock Wharf, south bank of James River, west of Smithfield, Virginia.
   5. Adapertural view showing prominent axial sculpture and seven spiral keels.
   6. Apertural view.
   7. Apical view showing prominent sculpture and heterostrophic protoconch.

8. *Carinorbis lyra* (Conrad) (*Fossarus lyra* of Dall, 1892, pl. 18, fig. 3a). 4 mm, locality not given. An artistic error added an extra rib to the body whorl for a total of eight. The aperture is correctly depicted.

9. *Carinorbis clathrata* (Philippi, 1844) (*Clathrella clathrata* of Cavallo and Repetto, 1992, p. 154-5, fig. 433).

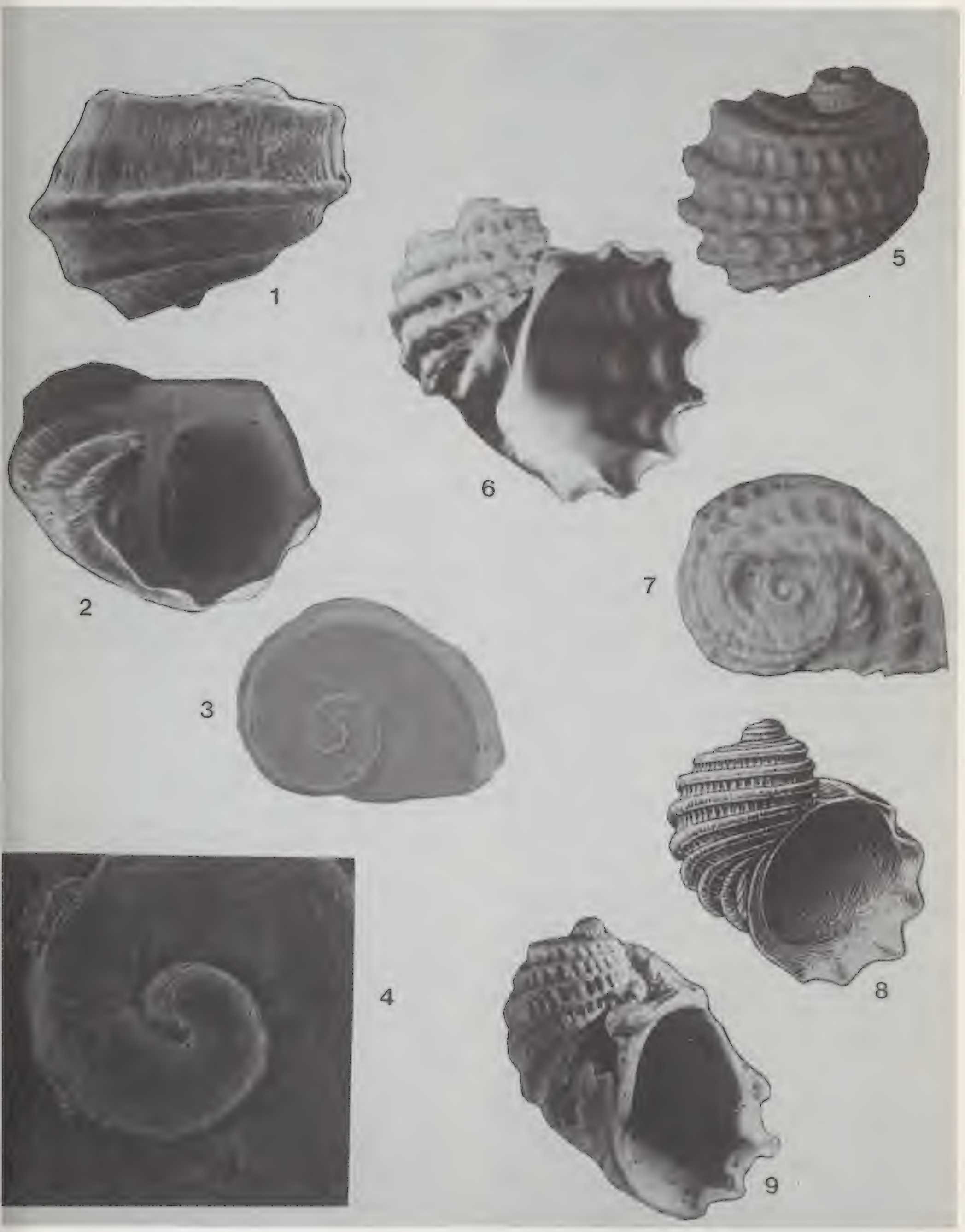

PLATE 1

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V. APPENDIX I: MOLLUSCS AND ECHINODERMS OF THE DUPLIN STRATOTYPE LOCALITY AT NATURAL WELL

BIVALVIA

Nucula proxima Say, 1822
UNC 15051

Nuculana acuta (Conrad, 1832)
UNC 15052

Anadara carolinensis (Dall, 1897)
Gardner, 1943 [1944]

Anadara callicestosa (Dall, 1898)
UNC 15053

Anadara improcera (Conrad, 1845)
UNC 15054

Anadara improcera bucula (Conrad, 1845)
UNC 15055

Anadara lienosa (Say, 1832)
UNC 15056

Noetia incile (Say, 1824)
UNC 15057

Noetia trigintinaria (Conrad, 1862)
UNC 6477

Glycymeris americana (Defrance, 1826)
UNC 1777

Glycymeris duplinensis Dall, 1898
UNC 15058

Glycymeris subovata (Say, 1824)
UNC 1778, 6457, 7534

Perna conradinus (Orbigny, 1852)
UNC 1756

Modiolus inflatus (Tuomey and Holmes, 1856)
UNC 15059

Carolinapecten eboreus (Conrad, 1833)
UNC 15060

Lima carolinensis Dall, 1898
UNC 15061

Plicatula marginata Say, 1824
UNC 1753, 3589, 15062

Ostrea compressirostra Say, 1824
UNC 15063

Ostrea sculpturata Conrad, 1840
UNC 1762

Placuanomia plicata Tuomey and Holmes, 1855
UNC 15064

Parvilucina trisulcata (Conrad, 1841)
UNC 15065

Parvilucina multilineata (Tuomey and Holmes, 1856)
UNC 15066

Parvilucina crenulata (Conrad, 1840)
UNC 15067

Callucina keenae Chavan, 1971
UNC 15068

Ctena speciosa (Rogers and Rogers, 1837)
Gardner, 1943 [1944]

Ctena microimbricata Gardner, 1943 [1944]
Gardner, 1943 [1944]

Pseudomiltha anodonta (Say, 1824)
UNC 15069

Diplodonta conradi McGavock, 1944
Gardner, 1943 [1944]

Diplodonta nucleiformis (Wagner, 1838)
UNC 15070

Chama congregata Conrad, 1833
UNC 1781

Chama corticosa Conrad, 1833
Gardner, 1943 [1944]

Chama emmonsi Nicol, 1953
UNC 1781a

Erycina carolinensis Dall, 1900
Gardner, 1943 [1944]

Aligena rhomboidea Gardner, 1943 [1944]
Gardner, 1943 [1944]

Bornia triangula Dall, 1900
UNC 15071

Mysella stantoni (Dall, 1900)
Gardner, 1943 [1944]

Sportella constricta (Conrad, 1841)
UNC 15072

Ensitellops protexta (Conrad, 1841)
UNC 15073

Carditamera arata (Conrad, 1832)
UNC 1775, 6478

Pleuromeris tridentata (Say, 1826)
UNC 15074

Pleuromeris tridentata decemcostata Conrad, 1867
UNC 15075

Pteromeris perplana (Conrad, 1841)
UNC 15076

Pteromeris perplana abbreviata (Conrad, 1841)
UNC 15077

Astarte concentrica Conrad, 1834
UNC 15078

Astarte undulata Say, 1824
UNC 15079

Eucrassatella speciosa (A. Adams, 1852)
UNC 15080

Eucrassatella virginica (Gmelin, 1791)
UNC 1755

Crassinella dupliniana (Dall, 1903)
UNC 15081

Crassinella lunulata (Conrad, 1834)
UNC 15082

Trigoniocardia (Americardia) media (Linnaeus, 1758)
UNC 15083

Clinocardium (Planicardium) acutilaqueatum (Conrad, 1839)
UNC 15084

Laevicardium sublineatum (Conrad, 1841)
UNC 15085

Laevicardium (Dinocardium) robustum (Lightfoot, 1786)
UNC 15086

Spisula duplinensis Dall, 1898
Gardner, 1943 [1944]

Mulinia congesta (Conrad, 1833)
UNC 1765

Note: The UNC collection contains two small *Mulinia* specimens among thousands present that have an adult *Mulinia lateralis* (Say, 1822) morphology. How-

ever, that species is typical of younger deposits, and the highly variable *M. congesta* can converge with it. Therefore, we do not believe the material in hand constitutes a certain record of *M. lateralis* from the Natural Well site.

Ervilia lata Dall, 1898
Gardner 1943 [1944]
Ensis directus (Conrad, 1843)
UNC 15087
Ensis ensiformis (Conrad, 1843)
UNC 15088
Tellina declivis Conrad, 1834
UNC 15089
Tellina dupliniana Dall, 1900
UNC 15090
Tellina macilenta Dall, 1900
Gardner, 1943 [1944]
Tellina umbra Dall, 1900
UNC 15091
Hemimetis magnoliana (Dall, 1900)
UNC 1715
Donax cuneola Gardner and Aldrich, 1919
UNC 15092
Donax emmonsi Dall, 1892
Gardner, 1943 [1944]
Semele carinata (Conrad, 1830)
UNC 15093
Semelina nuculoides (Conrad, 1841)
UNC 15094
Solecurtus cumingianus (Dunker, 1861)
UNC 15095
? *Corbicula densata* (Conrad, 1844)
UNC 15096 (shell preservation different from remaining collection.)
Mercenaria corrugata (Lamarck, 1818)
UNC 1760, 1774
Mercenaria sp.
UNC 1760a
Chione cribraria (Conrad, 1843)
UNC 1779, 6463, 6464
Chione latilirata (Conrad, 1841)
UNC 15097
Chione grus (Holmes, 1858)
UNC 15098
Gouldia metastriata (Conrad, 1838)
UNC 15099
Transanella carolinensis Dall, 1903
UNC 15100
Macrocallista greeni Ward and Blackwelder, 1987
UNC 15101
Gemma magna Dall, 1903
UNC 15102
Cooperella parilis (Conrad, 1875 [1873])
Gardner, 1943 [1944]
Sphenia dubia (H.C. Lea, 1843)
UNC 15103
Corbula inaequalis Say, 1824
UNC 15104
Corbula contracta Say, 1824
UNC 15105
Corbula retusa Gardner, 1943 [1944]
UNC 15106
Corbula sp.
UNC 15107
Gastrochaena ligula H.C. Lea, 1843
UNC 15108
Panopea reflexa Say, 1824
UNC 15109
Margaritaria abrupta (Conrad, 1832)
UNC 15110
Verticordia emmonsi Conrad, 1862
Gardner, 1943 [1944]

SCAPHOPODA
Dentalium eboreum Conrad, 1846
UNC 15111
Cadulus new species
UNC 15112

GASTROPODA
Diodoru carolinensis Conrad, 1875 [1873]
Gardner, 1948
Diodora nucula (Dall, 1892)
UNC 15113
Calliostoma sp., cf. *C. bella* (Conrad, 1834)
UNC 15114
Calliostoma labrosa (Conrad, 1834)
UNC 15115
Calliostoma virginica Conrad, 1875 [1873]
UNC 15116
Tegula exoluta (Conrad, 1843)
UNC 751
Arene tricatenaria (Stearns, 1872)
UNC 15117
Arene sp.
UNC 15118
Skenea harrisi (Olsson, 1916)
UNC 15119
Skenea smithfieldensis (Olsson, 1916)
UNC 15120
Omalogyra sp.
UNC 15121
Alvania lipeus (Dall, 1892)
UNC 15122
Cyclostremiscus obliquestriatus (H.C. Lea, 1843)
UNC 15123
Cyclostremiscus schmidti (Olsson, 1916)
UNC 15124
Aorotrema cistronium (Dall, 1889)
UNC 15125
Parviturboides sp.
UNC 15126
Teinostoma alexanderi (Olsson, 1916)
Olsson, 1916
Teinostoma bushi (Olsson, 1916)
UNC 15127
Teinostoma caloosaense Dall, 1892
UNC 15128
Teinostoma miocenica Olsson, 1916
Olsson, 1916
Teinostoma nana (I. Lea, 1833)
UNC 15129

Teinostoma subconica (H.C. Lea, 1843)
UNC 15130
Teinostoma thompsoni Olsson, 1916
Olsson, 1916
Teinostoma umbilicata (H.C. Lea, 1843)
UNC 15131
Macromphalina aperta (H.C. Lea, 1843)
Gardner, 1948
Caecum compactum Dall, 1892
UNC 15132
Caecum cooperi S. Smith, 1862
UNC 15133
Caecum ibex Dall, 1892
UNC 15134
Caecum new species
UNC 15135
Turritella burdeni (Tuomey and Holmes, 1856)
UNC 1312
Turritella etiwanensis (Tuomey and Holmes, 1856)
UNC 1780
Turritella fluxionalis Rogers and Rogers, 1837
UNC 15136
Turritella holmesi Dall, 1892
UNC 1312a
Turritella virginica Campbell, 1993
UNC 15137
Serpulorbis granifera (Say, 1824)
UNC 15138
Petaloconchus sculpturatus H.C. Lea, 1843
UNC 6475
Cerithiopsis bicolor (C.B. Adams, 1845)
UNC 15139
Cerithiopsis scariphus Dall, 1892
UNC 15140
Cerithiopsis smithfieldensis Olsson, 1916
UNC 15141
Seila adamsi (H.C. Lea, 1845)
UNC 15142
Triphora bartschi (Olsson, 1916)
UNC 15143
Triphora submonilifera (Orbigny, 1852)
UNC 15144
Epitonium aciculum (H.C. Lea, 1843)
UNC 15145
Epitonium duplinianum (Olsson, 1916)
Olssson, 1916
Epitonium fasciatum Gardner, 1948
Gardner, 1948
Epitonium junceum Gardner, 1948
Gardner, 1948
Epitonium magnolianum (Olsson, 1916)
Olsson, 1916
Epitonium micropleurum (H.C. Lea, 1843)
UNC 15146
Melanella laevigata (H.C. Lea, 1843)
UNC 15147
Melanella angulata (H.C. Lea, 1843)
UNC 15148
Melanella conchita Olsson and Harbison, 1953
UNC 15149
Strombiformis biconica Gardner, 1948
Gardner, 1948
Strombiformis lina Gardner, 1948
Gardner, 1948
Strombiformis migrans (Conrad, 1846)
UNC 15150
Strombiformis spatula Gardner, 1948
Gardner, 1948
Carinorbis lyra (Conrad, 1834)
UNC 15151
Carinorbis quadricostata (Emmons, 1858)
UNC 15152
Calyptraea centralis (Conrad, 1841)
UNC 744
Crucibulum auriculum spinosum (Sowerby, 1824)
UNC 746
Crucibulum grande (Say, 1824)
UNC 15153
Crucibulum scutellatum (Wood, 1828)
UNC 15154
Crepidula aculeata (Gmelin, 1791)
UNC 758
Crepidula cymbaeformis (Conrad, 1844)
UNC 15155
Crepidula fornicata (Linnaeus, 1758)
UNC 1761
Crepidula plana (Say, 1822)
UNC 15156
Siphocypraea carolinensis (Conrad, 1841)
UNC 1769
Erato maugeriae Gray, 1832
UNC 15157
Euspira interna (Say, 1824)
UNC 1754b
Euspira sayana Campbell, 1993
UNC 1754a
Neverita duplicatus (Say, 1822)
UNC 1771
Natica plicatella Conrad, 1863
UNC 15158
Tectonatica psila (Say, 1822)
UNC 15159
Sconsia hodgei (Conrad, 1841)
UNC 6472
Murexiella shilohensis (Heilprin, 1888)
UNC 15160
Urosalpinx lepidota (Dall, 1890)
UNC 15161
Urosalpinx trossula (Conrad, 1832)
UNC 15162
Pterorytis umbrifer (Conrad, 1832)
UNC 15163
Typhis harrisi Olsson, 1914
UNC 15164
Anachis styliola Dall, 1892
UNC 15165
Anachis obesa (C.B. Adams, 1845)
Gardner, 1948
Anachis parvulus (H.C. Lea, 1843)
UNC 15166

Strombina anomala (Gardner and Aldrich, 1919) Gardner, 1948
Mitrella communis (Conrad, 1862)
UNC 15167
Mitrella edenensis Richards and Harbison, 1947
UNC 15168
Mitrella matsoni (Mansfield, 1924)
UNC 15169
Aesopus ithitoma (Dall, 1890)
UNC 15170
Aesopus stearnsi (Tryon, 1883)
UNC 15171
Juliamitrella gardnerae (Blackwelder and Ward, 1987)
UNC 15172
Ptychosalpinx multirugata (Conrad, 1841) Gardner, 1948
Tritonoharpa floridensis Tucker and Wilson, 1932
Gardner, 1948
Celatoconus nux (Dall, 1892)
UNC 15173
Busycon canaliferum Conrad, 1863
UNC 15174
Busycon incile (Conrad, 1833)
UNC 15175
Busycon maximum (Conrad, 1839)
UNC 15176
Busycon excavatum (Conrad, 1840)
UNC 15177
Busycon contrarium (Conrad, 1840)
UNC 15230
Nassarius consenoides (Olsson, 1916) Olsson, 1916
Nassarius cornellianus (Olsson, 1916)
UNC 15178
Nassarius quadrulatus (H.C. Lea, 1843)
UNC 15179
Nassarius smithianus (Olsson, 1916) Olsson, 1916
Nassarius vibex (Say, 1822)
UNC 15180
Ilyanassa granifera (Conrad, 1868)
UNC 15181
Ilyanassa harpuloides (Conrad, 1844) Gardner, 1948
Ilyanassa johnsoni (Dall, 1892) Gardner, 1948
Ilyanassa scalaspira (Conrad, 1868)
UNC 15182
Ilyanassa sexdentata (Conrad, 1843) Gardner, 1948
Trajana pyta Gardner, 1948 Gardner, 1948
Fasciolaria rhomboidea Rogers and Rogers, 1839
UNC 15183
Terebraspira sparrowi Emmons, 1858 Gardner, 1948
Triplofusus gigantea (Kiener, 1840)
UNC 1759
Fusinus equalis (Emmons, 1858)
UNC 15184
Hesperisternia filicata (Conrad, 1843)
UNC 15185
Oliva canaliculata H.C. Lea, 1843
UNC 1750b
Oliva carolinensis (Conrad, 1863)
UNC 15186
Olivella ancillariaeformis (H.C. Lea, 1843)
UNC 15187
Olivella carolinae Gardner, 1948
UNC 15188
Olivella mutica (Say, 1822)
UNC 745
Olivella sp.
UNC 15189
Pleioptygma carolinensis (Conrad, 1841)
UNC 15190
Vexillum elaboratum (H.C. Lea, 1843)
UNC 15191
Vexillum reticulatum (Emmons, 1858)
UNC 15192
Scaphella trenholmi (Tuomey and Holmes, 1856)
UNC 15193
Aurinia obtusa (Emmons, 1858) Gardner, 1948
Bullata antiqua (Redfield, 1852)
UNC 15194
Bullata oliviformis (Tuomey and Holmes, 1856) Gardner, 1948
Dentimargo aureocincta (Stearns, 1872)
UNC 15195
Dentimargo eburneola (Conrad, 1834)
UNC 15196
Dentimargo schmidti (Olsson, 1916)
UNC 15197
Prunum limatulum (Conrad, 1834)
UNC 743
Prunum virginianum Conrad, 1868
UNC 743a
Prunum precursor (Dall, 1890)
UNC 15198
Granula lavalleeana (Orbigny, 1842)
UNC 15199
Persicula ovula Conrad, 1870
UNC 743b
Granulina virginica Campbell, 1993
UNC 15200
Granulina new species, aff. *G. hadra* (Dall, 1889)
UNC 15201
Volvarina tersa (Mansfield, 1930)
UNC 15202
Conus adversarius Conrad, 1841
UNC 1768
Conus marylandicus Green, 1830
UNC 1768a
Terebra carolinensis (Conrad, 1841)
UNC 15203
Terebra indenta Conrad, 1863
UNC 15204
Terebra unilineata (Conrad, 1841)

UNC 1751b
Mitrolumna mitrodita (Gardner and Aldrich, 1919)
UNC 15205
Drillia ecphorae Olsson, 1916
Olsson, 1916
Drillia emmonsi Olsson, 1916
Gardner, 1948
Drillia gastrophila Olsson, 1916
Olsson, 1916
Drillia mcgrawensis Olsson, 1916
Olsson, 1916
Drillia magnoliana Olsson, 1916
Olsson, 1916
Drillia precursor Gardner and Aldrich, 1919
UNC 15206
Drillia sumterensis Gardner and Aldrich, 1919
UNC 15207
Crassispira (Crassispirella) virginiana (Conrad, 1834)
UNC 15208
Cerodrillia simpsoni (Dall, 1887)
UNC 15209
Splendrillia tiara (Gardner, 1948)
UNC 15210
Cymatosyrinx lunata (H.C. Lea, 1843)
UNC 15211
Cymatosyrinx ziczac Gardner, 1948
Gardner, 1948
Cryoturris magnoliana (Olsson, 1916)
UNC 15212
Glyphostoma zoster Gardner, 1948
Gardner, 1948
Longchaeus suturalis (H.C. Lea, 1843)
UNC 15213
Odostomia (Odostomia) turbinopsis (H.C. Lea, 1843)
UNC 15214
Odostomia (Chrysallida) granulata (H.C. Lea, 1843)
UNC 15215
Odostomia (Menestho) milium (H.C. Lea, 1843)
UNC 15216
Odostomia (Evalea) diaphana (H.C. Lea, 1843)
UNC 15217
Odostomia spp. 1-3
UNC 15218-15220
Turbonilla spp. 1-3
UNC 15221-15223
Cyclostremella magnoliana Olsson, 1916
Olsson, 1916
Ringicula floridana Dall, 1889
UNC 15224
Acteocina candei (Orbigny, 1842)
UNC 15225
Acteocina lepta Woodring, 1928
UNC 15226
Cylichna duplinensis (Dall, 1896)
Gardner, 1948

ECHINODERMATA
Arbacia species (spine)
UNC 15227
Mellita species (fragments)
UNC 15228
Echinocardium orthonotum (Conrad, 1843)
UNC 15229

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AN UNUSUAL *NAYADINA* (BIVALVIA:MALLEIDAE) FROM THE EOCENE OF SOUTH CAROLINA

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Nayadina (Exputens) is a North American, Eocene, warm-water, malleid bivalve with Old World Tethyan affinities. Three species are known, and the one with the most widespread distribution is *N. (E.) batequensis* Squires, 1990, from northwestern Jamaica, the southern part of Baja California, Mexico, and western Washington. In Jamaica, the age of this species is only generally known as Early to Middle Eocene, but elsewhere its age is considered Early Eocene (Squires, 1990, 1992; Squires and Goedert, in press). The second species is the Early to Middle Eocene *N. (E.) llajasensis* (Clark, 1934) from southern and central California, central Oregon, and western Washington (Squires, 1990, 1992). The third species is the Middle to Late Eocene *N. (E.) ocalensis* (MacNeil, 1934) from Florida, Georgia, and North Carolina (Squires, 1990). Specimens of *Nayadina (Exputens)* sp., recently discovered in South Carolina by D. Campbell (this volume), may also represent *N. (E.) ocalensis*.

Exputens either immigrated into North America from the Old World via the circum-equatorial current that flowed east to west during the Early Eocene or the subgenus originated in the Jamaica area (Squires, 1992).

Recent preparation and study of a well-preserved single valve of a malleid specimen, which has been housed in the collections at the Florida Museum of Natural History (UF) for many years, revealed that the bivalve is a *Nayadina (Exputens)*. The specimen (UF 66044) was collected in 1975 by Muriel Hunter and Joseph Banks from a large boulder on the floor of the Martin Marietta Berkeley Quarry, Berkeley County, southern South Carolina. The quarry, which is about 75 km northwest of Charleston and 2.4 km south of the intersection of Route 6 and Route 59, near the town of Eutaw Spring, is shown on the U. S. Geological Survey, 7.5-minute, Cross Quadrangle, 1987 edition. The specimen is from the Santee Limestone and was embedded in a gray, well-indurated bioclastic limestone containing other bivalves, the large benthic foraminifera *Lepidocylina*, and fragments of bryozoans. No other complete valves of *Exputens* were found in the quarry although numerous fragments were detected.

Harris and Zullo (1980, fig. 3) correlated the Santee Limestone to the entire Claiborne Stage (Middle Eocene) of the Gulf Coast. They also interpreted this limestone to be composed of calcareous bank deposits that accumulated on a broad, low-lying foreland area over which the sea transgressed rapidly. Ward *et al.* (1979) designated the neostratatype for the Santee Limestone to be the Berkeley Quarry.

Specimen UF 66044 is 20.5 cm in length and 11.5 cm in height. It is about four times as large as any previously known specimen of *Nayadina (Exputens);* namely, a 5.38 cm long specimen of *N. (E.) llajasensis* from southern California. The valve of specimen UF 66044 has a prominently curved shape, with a peculiar pincher-like anterior end (plate 1, figures 1, 2). The posterior end is quadrate. The valve is moderately smooth except on its medial area where weathering has exposed irregular commarginal lamellae. The beak is prosogyrate, very low, and in the middle of the anterior half of the valve. The ligamental pit is 3 cm in length (measured parallel to the hinge), and a narrow byssal sinus is detectable in the beak area (plate 1, figure 3). The hinge area is flat and smooth posteriorly to the ligamental pit but is thickened and projecting anteriorly.

Squires (1990) showed that *Exputens*

had an epifaunal nestling mode of life, with attachment of the dorsal side (hinge side) by byssus to hard substrate, and a very wide range in morphologic variation. Specimen UF 66044 rested on the thickened portion of its hinge line that extended from the beak to the anterior end. Some elongation took place anteriorly but growth eventually began around some foreign object, like turtle grass, and resulted in the pincher-shaped anterior end. Posteriorly from the beak, the shell curved ventrally upward and outward.

Although UF 66044 differs from any known species of *Exputens* in regards to its large size and distinctive curved shape, we are reluctant to name a new species based on a single specimen of a bivalve that is well known for considerable morphologic variation. More specimens are needed to define fully this malleid from the Santee Limestone.

Specimen UF 66044 and those specimens referred to as *Nayadina (Exputens)* sp. by D. Campbell (this volume) represent the earliest records of *Exputens* in the southeastern United States and the first report of this subgenus in South Carolina.

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PLATE 1

Figures

1-3. *Nayadina (Exputens)* sp., right valve, length 20.5 cm, height 11.5 cm, UF 66044, from Santee Limestone (Middle Eocene), Martin Marietta Berkeley Quarry, Berkeley County, South Carolina.

1. Exterior, X 0.6.
2. Interior, X 0.6.
3. Close-up of hinge-line interior, X 1.

PLATE 1

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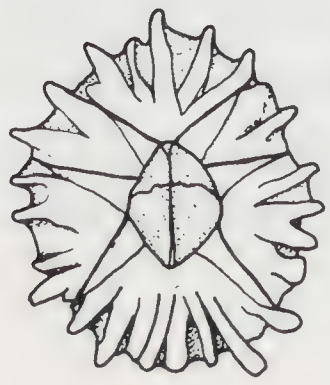

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RODOLFO F. J. BRUNET
PUERTO MADRYN, PROVINCIA DEL CHUBUT, ARGENTINA

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RODOLFO F. J. BRUNET
PUERTO MADRYN, PROVINCIA DEL CHUBUT, ARGENTINA

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I. ABSTRACT

The present work comprises the description and systematics of the Gastropoda and Scaphopoda obtained from the upper levels of the Entrerriense Formation, outcropping in Puerto Madryn and the Valdés Peninsula (Chubut Province, Argentina). Described and illustrated are 66 species of which 51 are new to the fauna, especially the Scaphopoda, a Class which previously has not had species described from here. This faunalistic association is tentatively assigned to the early Late Miocene, as revealed by the presence of typical warm water genera, with notable generic affinities to the Panamanian, Caribbean, and Neozelandic Bioprovinces, associated with paleoaustral and cosmopolitian genera.

II. INTRODUCTION

The sediments of the Entrerriense Formation outcropping in Puerto Madryn and the Valdés Peninsula (Chubut Province, Argentina) may be correlated with the

I. RESUMEN

El presente trabajo comprende la descripción y sistemática de los Gastropoda y Scaphopoda obtenidos en los niveles superiores de la Formación Entrerriense, aflorantes en Puerto Madryn y Península Valdés (Provincia del Chubut, Argentina). Se describen e ilustran 66 especies de las cuales 51 son nuevas para el contexto faunístico, especialmente los Scaphopoda, Clase de la que no ha sido descrita ninguna especie anteriormente. Esta asociación faunística es asignada tentativamente a los comienzos del Mioceno Superior, revelando la presencia de géneros típicos de aguas cálidas, con afinidades genéricas notorias respecto a las Bioprovincias panameña, caribeana y neozelandesa, asociados a géneros paleoaustrales y cosmopolitas.

II. INTRODUCCION

Las sedimentitas de la Formación Entrerriense aflorantes en Puerto Madryn y Península Valdés (Provincia del Chubut,

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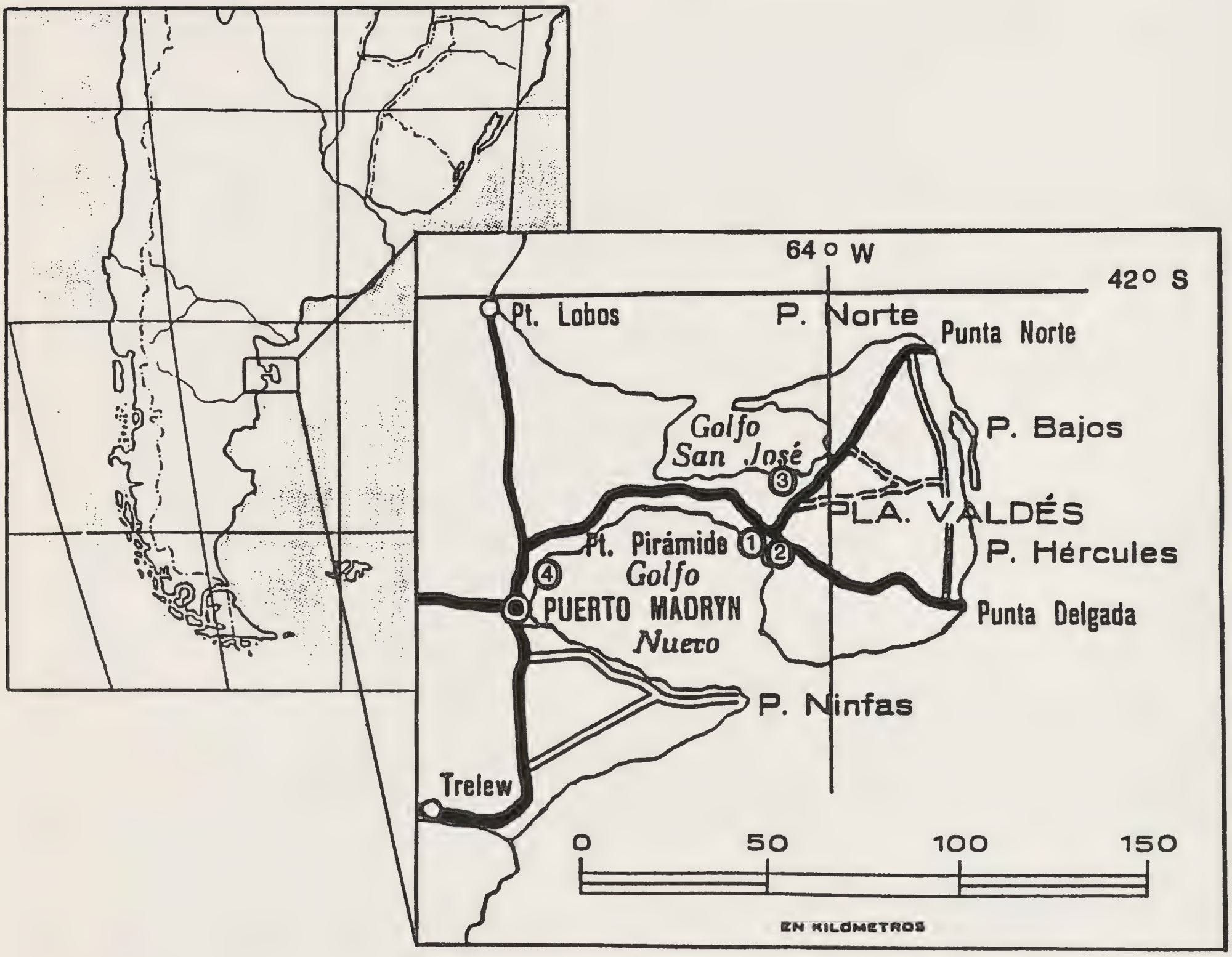

Text-figure 1. Map of Argentina, showing location of Valdés Peninsula. Insert map with fossil localities: 1) Puerto Pirámide; 2) Punta Pardela; 3) Playa Fracasso; 4) Baliza Punta Flecha.

Paraná Formation (Entre Rios), Camacho Formation (Uruguay), and those recorded from subsurface wells in Cuenca de Pelotas and Rio Grande (Brazil), and Laguna del Sauce and Chuy (Uruguay). Discrepancies exist with respect to the age, the stratigraphy, and the biostratigraphy. We consider that the knowledge of the fauna and especially of the biostratigraphy is still insufficient, but, we are inclined to place it tentatively between the end of the Middle Miocene and the beginning of the Late Miocene. The Entrerriense outcrops of South America have been studied by Darwin (1846), Doering (1882), F. Ameghino (1897, 1898, 1903, 1906), Borchert (1901), Rovereto (1913, 1921) Frenguelli (1926), Feruglio (1949), del Rio (1986, 1987, 1988, 1989, 1990, 1991) and Brunet (1986). Geologically the Tertiary sediments of Patagonia have been studied by some of

Argentina) son correlacionables con las de la Formación Paraná (Entre Ríos), Formación Camacho (Uruguay) y las registradas por perforaciones del subsuelo en la Cuenca de Pelotas y Rio Grande (Brasil), Laguna del Sauce y el Chuy (Uruguay). Existen discrepancias respecto a su edad, a su estratigrafía y a su bioestratigrafía. Nosotros consideramos que el conocimiento de su contexto faunístico y especialmente su bioestratigrafía es insuficiente aún, inclinandonos a ubicarla tentativamente entre el final del Mioceno Medio y los comienzos del Mioceno Superior. Los afloramientos entrerrienses de Sudamérica han sido estudiados por Darwin (1846), Doering (1882), F. Ameghino (1897, 1898, 1903, 1906), Borchert (1901), Rovereto (1913, 1921) Frenguelli (1926), Feruglio (1949), del Rio (1986, 1987, 1988, 1989, 1990, 1991) y Brunet

the aforementioned authors, who divide the beds into the Patagoniense, Entrerriense, and Rionegrense. Recently, Haller and Mendia (1980) named the basal unit the Gaiman Formation (Patagonian) and the overlying fossiliferous horizons (Entrerriense and Rionegrense) the Puerto Madryn Formation. Scasso and del Rio (1987) consider the three formations to be one unit. Although some authors (Ihering, 1907; del Rio, 1991) maintain that the typical fossiliferous horizons of the Entrerriense, bearing the fauna collected by Bravard (1858) in Paraná, have not yet been discovered in Patagonia, we believe that the upper levels of the Entrerriense Formation outcropping in Puerto Madryn, Puerto Pirámide, Punta Pardela, and Playa Fracasso, from which have been extracted the majority of our described examples, are completely correlative generically and specifically with those discovered in Paraná by Bravard.

III. ACKNOWLEDGMENTS

I wish to thank Dra. Emily Vokes for her enormous help in the critical reading of the manuscript and the valuable moral support that she offered to me. Likewise, I wish to express my thanks to Tulane University for having agreed to the publication of this work and to all the other persons who directly or indirectly have contributed to its realization.

IV. SYSTEMATIC PALEONTOLOGY

Class GASTROPODA
Order ARCHAEOGASTROPODA
Superfamily FISSURELLOIDEA
Family FISSURELLIDAE
Subfamily FISSURELLIDINAE
Genus FISSURELLIDEA Orbigny, 1841
FISSURELLIDEA aff. HIANTULA
(Lamarck, 1822)
Plate 1, figure 1

Description: Shell oblong, very depressed; wide central perforation, bordered by a strong callus. Ornamented exteriorly by fine and numerous radial striations. External flange lacking.

(1986). Geologicamente las sedimentitas terciarias de Patagonia han sido estudiadas por alguno de los autores antes mencionados, dividiendoselas en Patagoniense, Entrerriense y Rionegrense. Ultimamente Haller y Mendia (1980) denominaron a los términos basales Formación Gaiman (Patagoniano) y a los horizontes fosilíferos que las suprayacen (Entrerriense y Rionegrense) Formación Puerto Madryn. Scasso y del Rio (1987) consideran a las tres formaciones primigénitas como una sola. Si bien algunos autores (Ihering, 1907; del Rio, 1991) sostienen que los típicos horizontes fosilíferos del Entrerriense portadores de la fauna recolectada por Bravard (1858) en Paraná no han sido descubiertos aún en Patagonia, nosotros creemos que los niveles superiores de la Formación Entrerriense aflorantes en Puerto Madryn, Puerto Pirámide, Punta Pardela y Playa Fracasso de los que hemos extraído la mayoría de nuestros ejemplares descritos son perfectamente correlacionables genérica y especificamente con los descubiertos en Paraná por Bravard.

III. RECONOCIMIENTOS

Deseo agradecer a la Dra. Emily Vokes su enorme ayuda en la lectura crítica de los manuscritos y al valioso apoyo moral que me ha brindado. Asimismo expreso mi agradecimiento a la Universidad de Tulane por haber accedido a la publicación de este trabajo y a todas las demás personas que directa o indirectamente han contribuído a su realización.

IV. PALEONTOLOGIA SISTEMATICA

Clase GASTROPODA
Orden ARCHAEOGASTROPODA
Superfamilia FISSURELLOIDEA
Familia FISSURELLIDAE
Subfamilia FISSURELLIDINAE
Género FISSURELLIDEA Orbigny, 1841
FISSURELLIDEA aff. HIANTULA
(Lamarck, 1822)
Lámina 1, figura 1

Descripción: Concha oblonga, muy deprimida; amplia perforación central, bordeada por un fuerte callo. Exteriormente ornamentada por finas y numerosas estriaciones radiales. Falta reborde externo.

Hypotype: MPEF-PI-001; length: 20 mm; width: 14.5 mm; height: 4 mm.

Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Discussion: The species described above does not differ fundamentally from *Fissurellidea (Fissurellidea) hiantula* (Lamarck, 1822); but comparing it with various living examples, we have observed that the Recent ones are, in general, more depressed, with finer and less elevated striations.

Genus MEGATEBENNUS Pilsbry, 1890

MEGATEBENNUS PARDELENSIS, n. sp.

Plate 1, figure 2

Description: Shell elliptical, moderately elevated, posterior margin somewhat wider than the anterior; foramen central, oblong, and large; elevated above the level of the shell. External ornamentation consisting of fine radial ribs, crossed by irregular growth lines. Interior with heavy marginal flange, labrum smooth, callus oval, with a slight anterior prolongation and two latero-posterior ones that are shaped like a shield.

Holotype: MPEF-PI-027; length: 22 mm; width: 12 mm; height: 5 mm. Foramen: length 5 mm, width 3 mm.

Type locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named thus for the collecting site.

Discussion: The genus *Megatebennus* Pilsbry, 1890, is known from the Pliocene to the Recent in the western United States and in Australia. For the Tertiary formations of Patagonia, only *Fissurellidea eurytreta* (Cossmann, 1899) is known from the Superpatagoniense of Yegua Quemada (Sta. Cruz) and in the living fauna, we may mention *Fissurellidea hiantula* (Lamarck, 1822). *Megatebennus pardelensis,* n. sp., differs from *Megatebennus bimaculata* (Dall, 1872), which has both extremes of equal width, heavier radial ribs, and a perfectly oval callus. *Megatebennus pardelensis* has the following indices: shell width /shell length: 0.6; foramen width / foramen length: 0.6; the percent relationship: foramen length/shell length: 23% and foramen width/shell width: 25%. But for *Megatebennus bimaculata,* the Recent California species they are: shell width /shell length: 0.58; foramen width/foramen length: 0.5 and the percent relationship: foramen length /shell length : 23% and foramen width/shell width: 27%.

Hipotipo: MPEF-PI-001; largo: 20 mm; ancho: 14,5 mm; altura: 4 mm.

Localidad: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Discusión: La especie descrita no difiere fundamentalmente de *Fissurellidea (Fissurellidea) hiantula* (Lamarck, 1822); pero comparándola con varios ejemplares vivientes, hemos podido observar que las actuales son en general más deprimidas, con estriaciones más tenues y menos elevadas.

Género MEGATEBENNUS Pilsbry, 1890

MEGATEBENNUS PARDELENSIS, n. sp.

Lámina 1, figura 2

Descripción: Concha elíptica, medianamente elevada, borde posterior algo más ancho que el anterior; foramen central, oblongo y grande; elevado sobre el nivel de la concha. Ornamentación externa constituída por finas costillas radiales, cruzadas por lineas de crecimiento irregulares. Interior con reborde marginal grueso, labro liso, callo oval, con una leve prolongación anterior y dos latero-posteriores que le dan forma de escudo.

Holotipo: MPEF-PI-027; largo: 22 mm; ancho: 12 mm; altura: 5 mm. Foramen: largo 5 mm, ancho 3 mm.

Localidad tipo: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por el sitio de recolección.

Discusión: El género *Megatebennus* Pilsbry, 1890, es conocido desde el Plioceno hasta la actualidad en el Oeste de los EE.UU. y en Australia. Para las formaciones terciarias de Patagonia, solo se conoce *Fissurellidea eurytreta* (Cossmann, 1899) del Superpatagoniense de Yegua Quemada (Sta. Cruz) y como viviente podemos mencionar a *Fissurellidea hiantula* (Lamarck, 1822). *Megatebennus pardelensis,* n. sp., difiere de *Megatebennus bimaculata* (Dall, 1872) por tener ésta ambos extremos de igual ancho, costillas radiales más gruesas y callo perfectamente oval. *Megatebennus pardelensis* tiene los siguientes índices: ancho concha/largo concha: 0,6; ancho foramen/largo foramen: 0,6; relacion porcentual largo foramen/ largo concha: 23% y ancho foramen/ancho concha: 25%. Mientras que para *Megatebennus bimaculata,* especie reciente de California, son: ancho concha/ largo concha: 0,58; ancho foramen/largo foramen: 0,5 y las relaciones porcentuales: largo foramen/largo concha: 23% y ancho foramen/ancho concha: 27%.

Superfamily PATELLOIDEA
Family LOTTIIDAE
Subfamily LOTTIINAE
Genus SCURRIA Gray, 1847
SCURRIA SCURRA (Lesson, 1841)
Plate 1, figure 3

Description: Shell high, conical; apex subcentral, aperture oval. Sculpture consisting of concentric striations more conspicuous than the radial ones.

Hypotype: MPEF-PI-138; length: 14 mm; width: 11 mm; height: 9 mm.

Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Discussion: The characters of the fossil specimens are the same as those of the type species *Scurria scurra* (Lesson, 1841), which is reported for the first time in the Tertiary of Patagonia.

Order MESOGASTROPODA
Superfamily HIPPONICOIDEA
Family HIPPONICIDAE
Genus HIPPONIX Defrance, 1819
HIPPONIX OLIGOCOSTATA, n. sp.
Plate 1, figure 4

Description: Shell small, conical-oblique, low. Apex posterior, submarginal. Protoconch dextral, smooth. External ornamentation formed by the radial ribs, 37 in number and very slightly bifurcate. Growth lines crossing the ribs forming inconspicuous nodules. Muscle scar in the form of a horseshoe open anteriorly.

Holotype: MPEF-PI-002; length: 13 mm; width: 11 mm; height: 6 mm.

Type locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the small number of ribs which it possesses, compared to the known species.

Discussion: The genus *Hipponix* Defrance, 1819, has not previously been noted for the Entrerriense Formation of South America. Feruglio (1954) described *Gadinia alascioi* from the Late Pliocene of Santa Cruz (Argentina). *Gadinia* Gray, 1824, is a synonym of *Trimusculus* Schmidt, 1818, and is placed in the Order Basommatophora, which should be considered a pulmonate gastropod. *Hipponix oligocostata*, n. sp., differs from *Hipponix costata* Erdmann and Morra, 1985, from the Patagoniense of Santa Cruz, in that the indices are: width/height: 4.25; length/width: 1.11; length/height: 4.75 for the latter; but for the former they are: width/height: 0.85; length/width: 1.18 and length/

Superfamilia PATELLOIDEA
Familia LOTTIIDAE
Subfamilia LOTTIINAE
Género SCURRIA Gray, 1847
SCURRIA SCURRA (Lesson, 1841)
Lámina 1, figura 3

Descripción: Concha alta, cónica; ápice subcentral, abertura oval. Escultura constituída por estrías concéntricas más notorias que las radiales.

Hipotipo: MPEF-PI-138; largo: 14 mm; ancho: 11 mm; altura: 9 mm.

Localidad: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Discusión: Los caracteres de los especímenes fósiles son coincidentes con los de la especie tipo *Scurria scurra* (Lesson, 1841), que es mencionada por primera vez para el Terciario de Patagonia.

Orden MESOGASTROPODA
Superfamilia HIPPONICOIDEA
Familia HIPPONICIDAE
Género HIPPONIX Defrance, 1819
HIPPONIX OLIGOCOSTATA, n. sp.
Lámina 1, figura 4

Descripción: Concha pequeña, cónica-oblicua, baja. Apice posterior, submarginal. Protoconcha dextral, lisa. Ornamentación externa dada por costillas radiales en número de 37, muy pocas bifurcadas. Las cruzan líneas de crecimiento que al pasar por las costillas forman nódulos poco notorios. Marca muscular en forma de herradura abierta anteriormente.

Holotipo: MPEF-PI-002; largo: 13 mm; ancho: 11 mm; altura: 6 mm.

Localidad tipo: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por el menor número de costillas que posee, respecto a la especie conocida.

Discusión: El género *Hipponix* Defrance, 1819, no ha sido aún mencionado para la Formación Entrerriense de Sudamérica. Feruglio (1954) describe para el Plioceno Superior de Santa Cruz (Argentina) *Gadinia alascioi*. *Gadinia* Gray, 1824, se denomina actualmente *Trimusculus* Schmidt, 1818, y se ubica en el Orden Basommatophora, por lo que se trataría de un gastrópodo pulmonado. *Hipponix oligocostata*, n. sp., difiere de *Hipponix costata* Erdmann y Morra, 1985, del Patagoniense de Santa Cruz, los índices son: ancho/altura: 4,25; largo/ancho: 1,11; largo/altura: 4,75 para este último; mientras que para el primero son: ancho/

height: 2.17. *Hipponix costata* has a larger number of ribs (approximately 50) and they are not bifurcate.

Family CAPULIDAE
Genus CAPULUS Montfort, 1810
CAPULUS LADYAE, n. sp.
Plate 1, figure 5

Description: Shell in the shape of a cap, very small but strong; low, because the apex is very curved toward the rear, exceeding the posterior margin, diminishing rapidly in thickness, ending broken, but one may clearly observe the protoconch. Peristome oval, labrum heavy, crenulated by the termination of the costae at that point. Interior with muscle scar in the form of a horseshoe, open anteriorly. External ornamentation consisting of radial ribs crossed by the growth lines, making them irregular, without a tendency to bifurcation.

Holotype: MPEF-PI-028; length: 6 mm; width: 5 mm; height: 2.5 mm.

Type locality: Playa Fracasso, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to my wife Lady Mabel Fernandez.

altura: 0,85; largo/ancho: 1,18 y largo/altura: 2,17. *Hipponix costata* tiene un mayor número de costillas (aproximadamente 50) y estas no son bifurcadas.

Familia CAPULIDAE
Género CAPULUS Montfort, 1810
CAPULUS LADYAE, n. sp.
Lámina 1, figura 5

Descripción: Concha en forma de gorro, muy pequeña pero fuerte; baja, debido a que el ápice se encuentra muy curvado hacia atrás, sobrepasando el borde posterior, va disminuyendo rapidamente de espesor, terminando roto, pero observandose claramente la protoconcha. Peristoma oval, labro grueso, crenulado por la terminación a ese nivel de las costulaciones. Interior con marca muscular en herradura, abierta anteriormente. Ornamentación externa constituída por costillas radiales que al cruzarse con las lineas de crecimiento, se hacen irregulares, sin tendencia a la bifurcación.

Holotipo: MPEF-PI-028; largo: 6 mm; ancho: 5 mm; altura: 2,5 mm.

Localidad tipo: Playa Fracasso, Península Valdés, Provincia del Chubut, Argentina.

PLATE 1

Figure — Page

1. FISSURELLIDEA aff. HIANTULA (Lamarck, 1822) 3
   MPEF-PI-001 (hypotype); length: 20 mm; width: 14.5 mm; height: 4 mm.
   Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.
2. MEGATEBENNUS PARDELENSIS, n. sp. 4
   MPEF-PI-027 (holotype); length: 22 mm; width: 12 mm; height: 5 mm.
   Foramen: length 5 mm, width 3 mm.
   Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.
3. SCURRIA SCURRA (Lesson, 1841) 5
   MPEF-PI-138 (hypotype); length: 14 mm; width: 11 mm; height 9 mm.
   Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
4. HIPPONIX OLIGOCOSTATA, n. sp. 5
   MPEF-PI-002 (holotype); length: 13 mm; width: 11 mm; height 6 mm.
   Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.
5. CAPULUS LADYAE, n. sp. 6
   MPEF-PI-028 (holotype); length: 6 mm; width: 5 mm; height: 2.5 mm.
   Locality: Playa Fracasso, Valdés Peninsula, Chubut Province, Argentina.
6. CALYPTRAEA DISCOIDALIS, n. sp. 8
   MPEF-PI-003 (holotype); width: 31 mm; height: 11.5 mm.
   Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
7, 8. CRUCIBULUM MULTICOSTATUM, n. sp. 9
   7. MPEF-PI-004 (holotype); length: 36 mm; width: 26 mm; height: 17 mm.
   8. MPEF-PI-005 (paratype); length: 34 mm; width: 29 mm; height: 17 mm.
   Locality of both: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

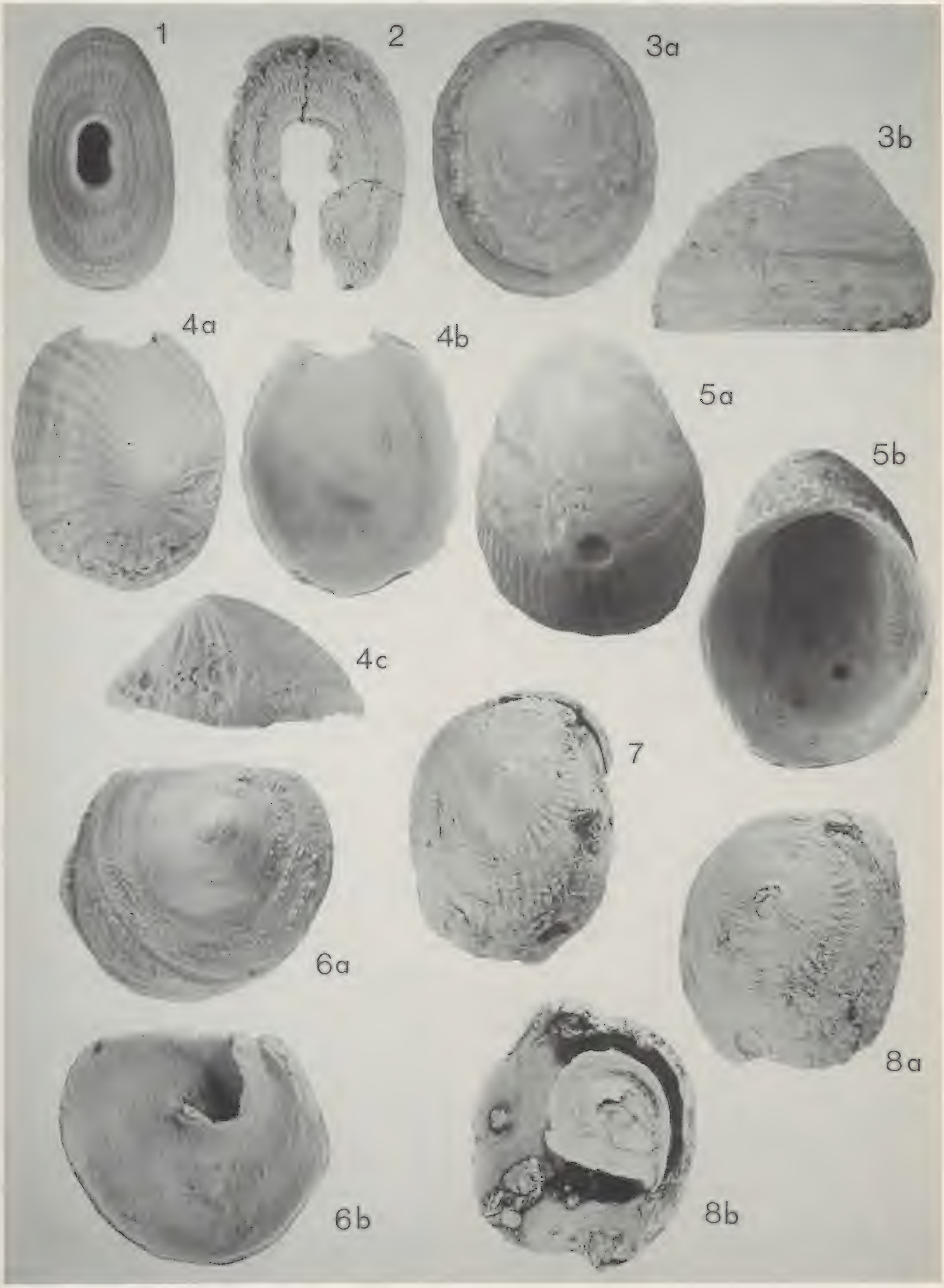

PLATE 1

Discussion: There is no record of the genus *Capulus* for the marine formations of the Tertiary of Patagonia. *Capulus ladyae,* n. sp., differs from *Capulus compressus* E.A. Smith, 1891, living on the Argentinian coast, which is of much larger size, very curved and much higher (8.5 x 8 x 2.5 mm), with a smooth peristome and compressed laterally. *Capulus ladyae* is somewhat similar to *Capulus incurvatus* (Gmelin, 1791) [= *Capulus contortus* (Lamarck, 1822)], but the latter differs by having a larger size (16 mm x 10 mm) (Rios, 1975) and better development of the growth lines relative to the ribs. It differs also from *Capulus hungaricus* (Linné, 1767), which has a much larger size, having the apex very incurved and the peristome strongly curved. *Capulus galea* Dall, 1889, has the peristome smooth and lacks the radial costae.

Superfamily CREPIDULOIDEA
Family CREPIDULIDAE
Genus CALYPTRAEA Lamarck, 1799
CALYPTRAEA DISCOIDALIS, n. sp.
Plate 1, figure 6

Description: Shell subcircular, conical, very low, with only two whorls. Apex smooth, subcentral, leaving the protoconch visible. First whorl less convex than the second. A spiral line visible and clear from the protoconch up to the first whorl; in the second, it is lost among the strong growth lines. Septum with slightly thickened margin, pseudo-columella very short.

Holotype: MPEF-PI-003; width: 31 mm; height: 11.5 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: So named because it is very flat.

Discussion: Until now there have been no specimens attributible to the genus *Calyptraea* Lamarck, 1799, from the Entrerriense Formation of South America. *Calyptraea discoidalis,* n. sp., differs from *Calyptraea costellata* Philippi, 1845 [= *Calyptraea pileus* Lamarck (Ihering, 1907)] of the Patagoniense of Santa Cruz (Argentina), which has stronger radial costae. Ihering (1907) proposed as *Calyptraea pileus juliana* a variety from San Julian, Santa Cruz, of the Lower Patagoniense, which is very flat; but differs from *Calyp-*

Derivatio nominis: Dedicado a mi esposa Lady Mabel Fernandez.

Discusión: No existe ninguna mención del género *Capulus* para las formaciones marinas del Terciario de Patagonia. *Capulus ladyae,* n. sp., difiere de *Capulus compressus* E.A. Smith, 1891, viviente en el litoral argentino, por ser ésta de mucho mayor tamaño, muy curvado y mucho más alto (8,5 x 8 x 2,5 mm), con peristoma liso y comprimido lateralmente. *Capulus ladyae* es algo similar a *Capulus incurvatus* (Gmelin, 1791) [= *Capulus contortus* (Lamarck, 1822)], pero difiere por tener ésta mayor tamaño (16 mm x 10 mm) (Rios, 1975) y mayor desarrollo de las lineas de crecimiento respecto a las costillas. Difiere también de *Capulus hungaricus* (Linné, 1767) por tener ésta mucho mayor tamaño, tener el ápice muy incurvado y el peristoma fuertemente curvado. Difiere de *Capulus galea* Dall, 1889, por tener ésta peristoma liso y ausencia de costulaciones radiales.

Superfamilia CREPIDULOIDEA
Familia CREPIDULIDAE
Género CALYPTRAEA Lamarck, 1799
CALYPTRAEA DISCOIDALIS, n. sp.
Lámina 1, figura 6

Descripción: Concha subcircular, cónica, muy baja, con solo dos vueltas. Apice liso, subcentral, dejando visible la protoconcha. Primera vuelta menos convexa que la segunda. Linea espiral visible y clara desde la protoconcha hasta primera vuelta; en la segunda, se pierde entre fuertes lineas de crecimiento. Septo con borde poco engrosado, pseudo-columela muy corta.

Holotipo: MPEF-PI-003; ancho: 31 mm; altura: 11,5 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominada así por ser muy plana.

Discusión: Hasta el presente no han sido descritos especímenes adjudicables al género *Calyptraea* Lamarck, 1799, para la Formación Entrerriense de Sudamérica. *Calyptraea discoidalis,* n. sp., difiere de *Calyptraea costellata* Philippi, 1845 [= *Calyptraea pileus* Lamarck (Ihering, 1907)] del Patagoniense de Santa Cruz (Argentina) por tener ésta fuertes costulaciones radiales. Ihering (1907) propone como *Calyptraea pileus juliana* a una variedad de San Julián, Santa Cruz, del

traea discoidalis in having numerous radial ribs. *Calyptraea americana* (Ortmann, 1900) differs in having a deep umbilical depression below which the septum is prolonged. *Calyptraea pileolus* d'Orbigny, 1841, living and also cited by Ihering (1907) from the Lower, Middle, and Upper Patagoniense, has a smaller diameter and a very elevated and conical shell. *Trochita araucana* Philippi, 1887, was described from an internal mold.

Patagoniense Inferior que es muy chata; pero difiere de *Calyptraea discoidalis* por tener numerosas costillas radiales. Difiere de *Calyptraea americana* (Ortmann, 1900), por tener ésta una profunda depresión umbilical sobre la que se prolonga el septo. *Calyptraea pileolus* d'Orbigny, 1841, viviente y también citada por Ihering (1907) para el Patagoniense Inferior, Medio y el Superpatagoniense, difiere por tener menor diámetro, concha muy elevada y cónica. *Trochita araucana* Philippi, 1887, ha sido descrita por un molde interno.

Genus CRUCIBULUM Schumacher, 1817

CRUCIBULUM MULTICOSTATUM, n. sp.

Plate 1, figures 7, 8

Description: Shell oval, conical, elevated. Apex small, smooth and pointed, subcentral and slightly curved. Cup in the form of a semicircle, compressed on one side and located at the interior wall of the shell. External ornamentation consisting of 50 very fine ribs all the way to the margin, which project above the margin giving a crenulated aspect, but not having relief in the shell interior. Fine irregular, concentric growth lines, which cross over the ribs, forming irregular rugosities.

Holotype: MPEF-PI-004; length: 36 mm; width: 26 mm; height: 17 mm.

Paratype: MPEF-PI-005; length: 34 mm; width: 29 mm; height: 17 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named thus for having a larger number of ribs than the only described Entrerriense species, *Crucibulum argentinum* (Philippi, 1893).

Discussion: Crucibulum multicostatum, n. sp., differs from *Crucibulum argentinum* (Philippi, 1893), which has only 20 to 22 fine ribs that begin at the apex, and widen gradually in the direction of the shell margin, projecting into the interior of the same. *Crucibulum argentinum* was described on the basis of an internal mold. The specimen described from the Camacho Formation (= Entrerriense Formation) of Uruguay, by Figueiras and Broggi (1971) also was based on internal and external molds, whose characteristics are coincident with those of *Crucibulum argentinum*.

Género CRUCIBULUM Schumacher, 1817

CRUCIBULUM MULTICOSTATUM, n. sp.

Lámina 1, figuras 7, 8

Descripción: Concha oval, cónica, elevada. Apice pequeño, liso y agudo, subcentral y algo curvado. Infundibulum en forma de semi-círculo, comprimido en uno de sus lados y unido a la pared interior de la concha. Ornamentación externa constituída por 50 costillas muy finas en toda su extensión, que se proyectan sobre el borde dándole un aspecto crenulado, pero no hacen relieve en el interior de la concha. Lineas de crecimiento concéntricas, finas e irregulares que pasan sobre las costillas, formando irregularidades rugosas.

Holotipo: MPEF-PI-004; largo: 36 mm; ancho: 26 mm; altura: 17 mm.

Paratipo: MPEF-PI-005; largo: 34 mm; ancho: 29 mm; altura: 17 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominada así por tener mayor número de costillas que la única especie Entrerriense descrita, *Crucibulum argentinum* Philippi, 1893.

Discusión: Crucibulum multicostatum, n. sp., difiere de *Crucibulum argentinum* (Philippi, 1893) por tener ésta solo 20 a 22 costillas finas que nacen del ápice, y se ensanchan paulatinamente al dirigirse al borde de la concha, proyectándose en el interior de la misma. *Crucibulum argentinum* ha sido descrito sobre un molde interno. El espécimen descrito para la Formación Camacho (= Formación Entrerriense) del Uruguay, por Figueiras y Broggi (1971) con moldes internos y externos, sus características, son coincidentes con las de *Crucibulum argentinum*.

Superfamily TROCHACEA
Family TROCHIDAE
Subfamily CALLIOSTOMATINAE
Genus CALLIOSTOMA Swainson, 1840
Subgenus CALLIOSTOMA s.s.
CALLIOSTOMA (CALLIOSTOMA) SUAREZI, n. sp.
Plate 2, figure 1

Description: Shell conical, pointed and somewhat elevated, not umbilicate; four and one-half whorls, the last angulate. Suture defined only by one very fine groove; peristome angulate and mouth subquadrate; columella concave, with two longitudinal plaits and terminal tuberosity. Ornamentation consisting of one double peripheral cord, and six granulose cords, alternating between heavy and fine; the last cord followed by one small groove. On the penultimate whorl one fine smooth cord and six granulose ones, alternating between heavy and fine. The whorls increasing rapidly in diameter, making the shell low and conical. Base slightly convex with seven flat cords.

Holotype: MPEF-PI-089; height: 7.3 mm; last whorl: width 8.5 mm, height 3.5 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the malacologist Sr. Alejandro Suarez.

Discussion: Calliostoma suarezi, n. sp., differs from *Calliostoma punctatulum* Borchert, 1901, which has the shell more elevated and less pointed, being ornamented only by granulose cords, numbering six on each whorl and with seven to nine basal cords, between which are intercalated finer ones. *Calliostoma puelchanum* Borchert, 1901, differs in having three heavy cords and two granulose ones on the last whorl and two smooth heavy cords with one granulose one on the penultimate whorl. *Calliostoma bravardi* Borchert, 1901, has eight heavy flat cords on the penultimate whorl and 13 heavy smooth ones on the base. *Calliostoma bonaerensis* Carral Tolosa, 1942, has the whorls separated by deep grooves, in which there are one or two smooth cords, and six spiral granulose cords on the last whorl; with three granulose and three smooth cords intercalated on the penultimate whorl.

CALLIOSTOMA (CALLIOSTOMA) NATIVUM, n. sp.
Plate 2, figure 2

Superfamilia TROCHACEA
Familia TROCHIDAE
Subfamilia CALLIOSTOMATINAE
Género CALLIOSTOMA Swainson, 1840
Subgénero CALLIOSTOMA s.s.
CALLIOSTOMA (CALLIOSTOMA) SUAREZI, n. sp.
Lámina 2, figura 1

Descripción: Concha cónica, puntuda y poco elevada, no umbilicada; cuatro y medio anfractos, el último anguloso. Suturas definidas solo por un surco muy fino; peristoma angulado y boca subcuadrada; columela cóncava, con dos pliegues longitudinales y una tuberosidad terminal. Ornamentación constituída por un cordón doble, periférico y seis cordones granulosos, alternados entre gruesos y finos; al último cordón le sigue un pequeño surco. En la penúltima vuelta hay un cordón fino, liso y seis cordones granulosos, alternados entre gruesos y finos. Las vueltas aumentan rapidamente de diámetro, lo que hace que la concha sea baja y cónica. Base poco convexa con siete cordones planos.

Holotipo: MPEF-PI-089; altura: 7,3 mm; último anfracto: ancho 8,5 mm, altura 3,5 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al malacólogo Sr. Alejandro Suarez.

Discusión: Calliostoma suarezi, n. sp., difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta concha más elevada y menos puntuda, estar ornamentado solo por cordones granulosos, en número de seis en cada vuelta y con siete a nueve cordones basales, entre los que se intercalan cordones mas finos. Difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones gruesos y dos granulosos en el último anfracto y dos cordones lisos, gruesos con un cordón granuloso en el penúltimo anfracto. Difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta ocho cordones gruesos y planos en el penúltimo anfracto y 13 cordones lisos y gruesos en la base. De *Calliostoma bonaerensis* Carral Tolosa, 1942, difiere por tener ésta los anfractos separados por surcos profundos de los que sobresalen una o dos cordones lisos y seis cordones espirales granulosos en el último anfracto; con tres granulosos y tres lisos intercalados en el penúltimo anfracto.

CALLIOSTOMA (CALLIOSTOMA) NATIVUM, n. sp.
Lámina 2, figura 2

Description: Shell small, trocoid and non-umbilicate; four and one-half well defined whorls. Peristome very angulose and crenulated, mouth subquadrate; columella almost straight; forming an angulosity with the anterior margin of the peristome. Ornamentation on the last whorl consisting of one perimetral cord, doubled and smooth, followed by seven granulose cords. The penultimate whorl beginning with one very fine smooth cord and four granulose cords. Base with 12 thin flat cords.

Holotype: MPEF-PI-090; height 7 mm; last whorl: width 5 mm, height 2.6 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: So named for being a typical Entrerriense species.

Discussion: Calliostoma nativum, n. sp., differs from *Calliostoma punctatulum* Borchert, 1901, which has six granulose cords on the last whorl and from seven to nine spiral ones on the base. *Calliostoma puelchanum* Borchert, 1901, has on the last whorl three heavy smooth cords and two granulose ones, and on the base from seven to ten flat spiral cords. *Calliostoma bravardi* Borchert, 1901, differs in having eight smooth flat cords on the last whorl and, on the base, 13 smooth flat ones. *Calliostoma doellojuradoi* Carral Tolosa, 1942, has 12 thin cords, smooth on the last whorl and granulose on the earlier whorls. It also differs from *Calliostoma bonaerensis* Carral Tolosa, 1942, which has deep sutural grooves, in which there are two smooth cords, and six spiral granulose cords on the last whorl.

Descripción: Concha pequeña, trocoide y anónfala; cuatro y medio anfractos bien delimitados. Peristoma muy anguloso y festoneado, boca subcuadrada; columela casi recta, formando angulosidad con el borde anterior del peristoma. Ornamentación del último anfracto constituída por un cordón perimetral doble y liso, al que le siguen siete cordones granulosos. El penúltimo anfracto comienza con un cordón muy fino y liso y cuatro cordones granulosos. Base con 12 cordones finos y planos.

Holotipo: MPEF-PI-090; altura 7 mm; último anfracto: ancho 5 mm, altura 2,6 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por ser una especie típica.

Discusión: Calliostoma nativum, n. sp., difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta seis cordones granulosos en el último anfracto y de siete a nueve cordones concéntricos en la base. Difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta en la última vuelta tres cordones gruesos y lisos y dos granulosos, y en la base de siete a diez cordones planos, espirales. De *Calliostoma bravardi* Borchert, 1901, difiere por tener ésta ocho cordones lisos y planos en la última vuelta y en la base 13 cordones lisos y planos. Difiere de *Calliostoma doellojuradoi* Carral Tolosa, 1942, por tener ésta 12 cordones lisos y finos en la última vuelta y granulosos en las primeras vueltas. También difiere de *Calliostoma bonaerensis* Carral Tolosa, 1942, por tener ésta surcos suturales profundos de los que sobresalen dos cordones lisos y seis cordones espirales granulosos en la última vuelta.

Calliostoma (Calliostoma) planum, n. sp.
Plate 2, figure 3

Description: Shell conical but very low; three and one-half whorls. Whorls almost flat but with visible groove, barely excavated; non-umbilicate; aperture subquadrate; umbilical callus with one final vertical fold; last whorl ornamented by one heavy convex smooth basal cord, which is followed by six to eight convex ones, less heavy and smooth, which have intercalated very fine cords, also smooth. On the penultimate whorl there are only six or seven consecutive cords, lacking the finer intercalated ones. Base with 14 thin smooth cords.

Holotype: MPEF-PI-091; height: 7 mm; last whorl: width 11 mm, height 4 mm.

Calliostoma (Calliostoma) planum, n. sp.
Lámina 2, figura 3

Descripción: Concha cónica pero muy baja; tres y media vueltas. Anfractos casi planos pero con surco visible, apenas excavado; anónfala; abertura subcuadrada; callo umbilical con uno o dos pliegues; columela cóncava con un repliegue final vertical; último anfracto ornamentado por un grueso cordón basal, convexo y liso al que le siguen de seis a ocho cordones convexos, menos gruesos y lisos que tienen intercalados muy finos cordones, también lisos. En el penúltimo anfracto se observan solo seis o siete cordones consecutivos, faltando los cordones más finos intercalados. Base con 14 cordones finos y lisos.

Holotipo: MPEF-PI-091; altura: 7 mm; último anfracto: ancho 11 mm, altura 4 mm.

PLATE 2

Figure Page

1. CALLIOSTOMA (CALLIOSTOMA) SUAREZI, n. sp. 10
MPEF-PI-089 (holotype); height: 7.3 mm; last whorl: width 8.5 mm, height 3.5 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
2. CALLIOSTOMA (CALLIOSTOMA) NATIVUM, n. sp. 10
MPEF-PI-090 (holotype); height: 7 mm; last whorl: width 5 mm, height 2.6 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
3. CALLIOSTOMA (CALLIOSTOMA) PLANUM, n. sp. 11
MPEF-PI-091 (holotype); height: 7 mm; last whorl: width 11 mm, height 4 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
4. CALLIOSTOMA (CALLIOSTOMA) MALUMIANI, n. sp. 14
MPEF-PI-092 (holotype); total height: 7 mm; last whorl: width 6.5 mm, height 3 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
5. CALLIOSTOMA (CALLIOSTOMA) MASIUKI, n. sp. 15
MPEF-PI-093 (holotype); total height: 8 mm; last whorl: width 6.4 mm, height 3 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
6. CALLIOSTOMA (CALLIOSTOMA) DUPLICATUM, n. sp. 16
MPEF-PI-094 (holotype); total height: 12.5 mm; last whorl: width 12.3 mm, height 6 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
7. CALLIOSTOMA (CALLIOSTOMA) MEISTERI, n. sp. 17
MPEF-PI-095 (holotype); total height; 6.5 mm; last whorl: width 6.6 mm, height 2.8 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
8. CALLIOSTOMA (CALLIOSTOMA) TROMBOTTOI, n. sp. 18
MPEF-PI-096 (holotype); total height: 4 mm; last whorl: width 6 mm, height 3 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
9. CALLIOSTOMA (CALLIOSTOMA) ARGENTINUM, n. sp. 18
MPEF-PI-097 (holotype); total height: 6 mm; last whorl: width 6mm, height 2.6 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
10. CALLIOSTOMA (CALLIOSTOMA) FIDALGOI, n. sp. 19
MPEF-PI-098 (holotype); total height: 6 mm; last whorl: width 5 mm, height 1.9 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
11. CALLIOSTOMA (CALLIOSTOMA) CAMINOSI, n. sp. 20
MPEF-PI-099 (holotype); total height: 5 mm; last whorl: width 6 mm, height 2.2 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
12. CALLIOSTOMA (CALLIOSTOMA) BONORINOI, n. sp. 20
MPEF-PI-100 (holotype); total height: 6 mm; last whorl: width 6.7 mm, height 3 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
13. CALLIOSTOMA (CALLIOSTOMA) NULLOI, n. sp. 21
MPEF-PI-101 (holotype); height: 4 mm (apex broken); last whorl: width 6.2 mm, height 2 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
14. CALLIOSTOMA (CALLIOSTOMA) CASTELLANOSAE, n. sp. 22
MPEF-PI-102 (holotype); total height: 16 mm; last whorl: width 12.1 mm, height 5 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

(Continued on p. 14)

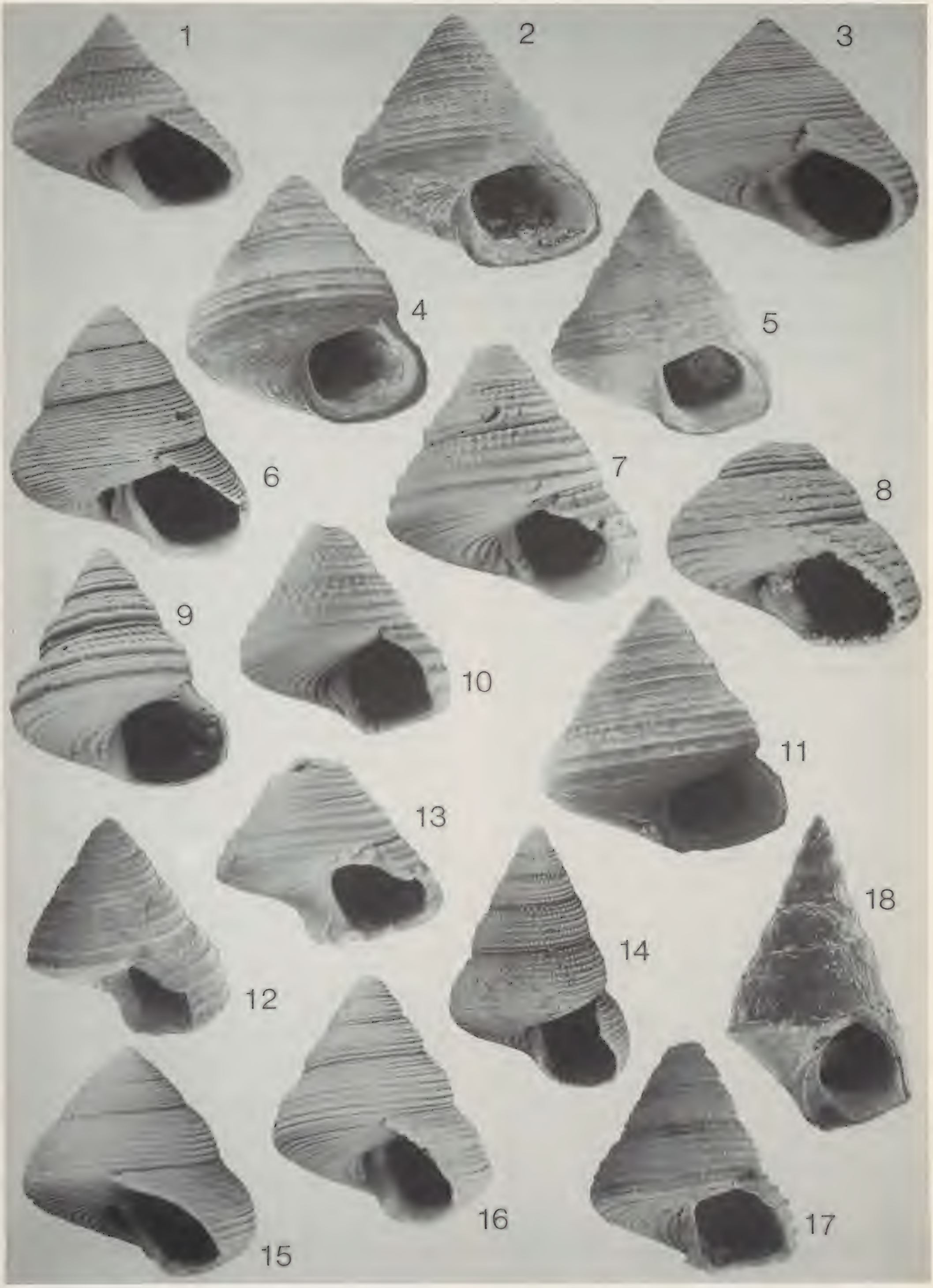

PLATE 2

15. CALLIOSTOMA (CALLIOSTOMA) MAPUCHEI, n. sp. 23
MPEF-PI-103 (holotype); total height: 12 mm; last whorl: width 16 mm, height 6.5 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
16. CALLIOSTOMA (CALLIOSTOMA) AMEGHINOI, n. sp. 23
MPEF-PI-104 (holotype); total height: 9.5 mm; last whorl: width 10.5 mm, height 3.2 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
17. CALLIOSTOMA (CALLIOSTOMA) PUNCTATULUM Borchert, 1901 24
MPEF-PI-105 (hypotype); total height: 8 mm; last whorl: width 6.5 mm, height 2 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
18. CALLIOSTOMA (FENEONIANA) STIPANICICI, n. sp. 25
MPEF-PI-139 (holotype); height: 5 mm; width: 3 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named thus for the limited height of the shell.

Discussion: Calliostoma planum, n. sp., differs from *Calliostoma bravardi* Borchert, 1901, which has 12 smooth flat cords on the last whorl; a higher form for the shell and has on the base 13 flat cords; lacking in this species is the umbilical callus and the two folds in the callus. *Calliostoma doellojuradoi* Carral Tolosa, 1942, has 12 fine cords, smooth on the last whorl and granulose on the earlier whorls. It is not comparable to *Calliostoma puelchanum* Borchert, 1901, *Calliostoma punctatulum* Borchert, 1901, *Calliostoma lepidum* (Philippi, 1893), or *Calliostoma bonaerensis* Carral Tolosa, 1942.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por la escasa altura de la concha.

Discusión: Calliostoma planum, n. sp., difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta 12 cordones lisos y planos en el último anfracto; por la forma más alta de la concha y tener en la base 13 cordones planos; faltando en esta especie el callo umbilical y los dos repliegues del callo. De *Calliostoma doellojuradoi* Carral Tolosa, 1942, difiere por tener ésta 12 cordones lisos y finos en la última vuelta y cordones granulosos en las primeras vueltas. No es comparable con *Calliostoma puelchanum* Borchert, 1901, con *Calliostoma punctatulum* Borchert, 1901, con *Calliostoma lepidum* (Philippi, 1893) ni con *Calliostoma bonaerensis* Carral Tolosa, 1942.

Calliostoma (Calliostoma) malumiani, n. sp.

Plate 2, figure 4

Description: Shell small, turbiniform; five and one-half angulate whorls, the last whorl biangulate. Suture slightly marked, peristome angulate, aperture subquadrate, base slightly convex, without umbilicus. Columella concave, without callus. Ornamentation on the last whorl formed by one smooth double peripherial cord, which is followed by one very narrow smooth band and one very fine smooth cord, then one heavy granulose cord, forming the upper angulation of the whorl, and two very fine granulose cords. The penultimate whorl has three smooth convex cords of equal size, one heavy granulose one and two finer granulose ones. Base with

Calliostoma (Calliostoma) malumiani, n. sp.

Lámina 2, figura 4

Descripción: Concha pequeña, turbiniforme; cinco y medio anfractos angulosos, el último biangulado. Suturas poco marcadas, peristoma anguloso, abertura subcuadrada, base poco convexa, sin ombligo. Columela cóncava, sin callosidad. Ornamentación del último anfracto formada por un doble cordón periférico liso, al que le sigue una banda lisa muy ancha y un cordón muy fino, liso, luego un cordón granuloso, grueso que forma la angulación superior del anfracto y dos cordones granulosos, muy finos. El penúltimo anfracto consta de tres cordones convexos y lisos de igual espesor, un cordón granuloso grueso y dos granulosos más finos. Base con nueve cordones finos y lineas de cre-

nine finer cords and oblique growth lines that converge on the umbilical zone.

Holotype: MPEF-PI-092; total height: 7 mm; last whorl: width 6.5 mm, height 3 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the Argentinian micropaleontologist Dr. Norberto Malumian.

Discussion: Calliostoma malumiani, n. sp., differs from *Calliostoma puelchanum* Borchert, 1901, which has three heavy smooth cords and two granulose ones on the last whorl, and a strong umbilical callus. *Calliostoma bravardi* Borchert, 1901, differs in having eight smooth cords on the last whorl and 13 smooth heavy cords on the base. *Calliostoma punctatulum* Borchert, 1901, has six granulose cords with finer and also granulose ones intercalated on the last whorl, and the base with seven to nine smooth spiral cords. *Calliostoma doellojuradoi* Carral Tolosa, 1942, has 12 smooth fine cords on the last whorl and the early whorls with granulose ones. *Calliostoma bonaerensis* Carral Tolosa, 1942, has the whorls separated by grooves, in which there are two smooth cords; and has six granulose cords on the last whorl and three granulose cords intercalated with three smooth ones on the penultimate whorl.

CALLIOSTOMA (CALLIOSTOMA) MASIUKI, n. sp.
Plate 2, figure 5

Description: Shell small, turbiniform, not umbilicate, whorls convex, the last biangulate. Aperture slightly angulate, but subquadrate. Columella almost straight, without umbilical depression. Ornamentation of the last whorl with one double perimetral cord, one thin flat cord, and six granulose cords, the first very fine and the second projecting, giving an angulation to the whorl; penultimate whorl with two fine smooth cords and five granulose cords, the first and the fourth very fine. Base slightly convex with 12 fine cords; without umbilical callus.

Holotype: MPEF-PI-093; total height: 8 mm; last whorl: width 6.4 mm, height 3 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the Argentinian geologist Dr. Vladimir Masiuk.

Discussion: Calliostoma masiuki, n. sp., differs from *Calliostoma punctatulum* Bor-

cimiento oblicuas que convergen en la zona umbilical.

Holotipo: MPEF-PI-092; altura total: 7 mm; último anfracto: ancho 6,5 mm, altura 3 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al micropaleontólogo argentino Dr. Norberto Malumian.

Discusión: Calliostoma malumiani, n. sp., difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones lisos y gruesos y dos cordones granulosos en el último anfracto, y un fuerte callo umbilical. Difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta ocho cordones lisos en el último anfracto y 13 cordones lisos y gruesos en la base. Difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta seis cordones granulosos con intercalación de otros más finos y también granulosos en la última vuelta, y base con siete a nueve cordones concéntricos, lisos. Difiere de *Calliostoma doellojuradoi* Carral Tolosa, 1942, por tener ésta 12 cordones lisos y finos en la última vuelta y las primeras, con cordones granulosos. Difiere de *Calliostoma bonaerensis* Carral Tolosa, 1942, por tener ésta anfractos separados por surcos de los que sobresalen dos cordones lisos; por tener seis cordones granulosos en la última vuelta y tres granulosos intercalados con tres lisos en la penúltima vuelta.

CALLIOSTOMA (CALLIOSTOMA) MASIUKI, n. sp.
Lámina 2, figura 5

Descripción: Concha pequeña, turbiniforme, no umbilicada, de vueltas convexas, la última biangulada. Abertura poco angulosa, pero subcuadrada. Columela casi recta, sin retracción umbilical. Ornamentación del último anfracto con un cordón doble perimetral, un cordón fino y plano y seis cordones granulosos, el primero muy fino y el segundo saliente, dándole angulación al anfracto; penúltimo anfracto con dos cordones finos y lisos y cinco cordones granulosos, el primero y el cuarto muy finos. Base levemente convexa con 12 cordones finos; sin callo umbilical.

Holotipo: MPEF-PI-093; altura total: 8 mm; último anfracto: ancho 6,4 mm, altura 3 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geológo argentino Dr. Vladimir Masiuk.

Discusión: Calliostoma masiuki, n. sp., difiere de *Calliostoma punctatulum* Bor-

chert, 1901, which has only six cords, intercalated fine and heavy, granulose on the last whorl, and one fine and five granulose cords on the penultimate whorl, without intercalation of fine ones; lacking an angulation on the basal whorl. *Calliostoma bravardi* Borchert, 1901, has only smooth, flat costae. *Calliostoma puelchanum* Borchert, 1901, has three very heavy, smooth cords and two granulose ones on the last whorl.

CALLIOSTOMA (CALLIOSTOMA) DUPLICATUM, n. sp.
Plate 2, figure 6

Description: Shell turbiniform, of medium size; five and one-half convex whorls; suture well delimited; last whorl without perimetral angulation; peristome slightly angulate, aperture subquadrate. Not umbilicate. Columella very curved with strong umbilical callus. Ornamentation of the last whorl consisting of nine flat double cords, on the penultimate whorl ten flat double cords, and on the antepenultimate only five flat double cords. Base with 13 flat double cords.

Holotype: MPEF-PI-094; total height: 12.5 mm; last whorl: width 12.3 mm, height 6 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: So named for having double spiral cords.

Discussion: Calliostoma duplicatum, n. sp., differs from *Calliostoma bravardi* Borchert, 1901, which has smaller size, and only eight flat spiral cords on the last whorl and 13 spiral cords on the base; the umbilical callus is much less developed. *Calliostoma doellojuradoi* Carral Tolosa, 1942, differs in having flat whorls, the last angulate, with 12 fine smooth cords, and with granulose cords on the early whorls. *Calliostoma bonaerensis* Carral Tolosa, 1942, has deep sutural grooves, in which there are two smooth cords; spiral cords granulose on the first whorl with smooth and granulose ones on the penultimate whorl. *Calliostoma puelchanum* Borchert, 1901, differs in having three heavy smooth cords on the last whorl, with two granulose ones, and on the penultimate two strong smooth cords, and one granulose one. *Calliostoma punctatulum* Borchert, 1901, has

chert, 1901, por tener ésta solo seis cordones, intercalados finos y gruesos, granulosos en el último anfracto y uno fino y cinco granulosos en el penúltimo, sin intercalación de cordones finos; carece de angulación en el anfracto basal. Difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta solo costillas lisas y planas. Difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones muy gruesos y lisos y dos cordones granulosos en el último anfracto.

CALLIOSTOMA (CALLIOSTOMA) DUPLICATUM, n. sp.
Lámina 2, figura 6

Descripción: Concha turbiniforme de mediano tamaño. Cinco y media vueltas, anfractos convexos; sutura bien delimitada; última vuelta sin angulación perimetral; peristoma poco anguloso, abertura subcuadrada. Sin ombligo. Columela muy curva con callo umbilical fuerte. Ornamentación del último anfracto constituída por nueve cordones planos y dobles, en la penúltima diez cordones planos y dobles, y en la antepenúltima solo cinco cordones planos y dobles. Base con 13 cordones planos y dobles.

Holotipo: MPEF-PI-094; altura total: 12,5 mm; último anfracto: ancho 12,3 mm, altura 6 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por tener cordones concéntricos dobles.

Discusión: Calliostoma duplicatum, n. sp., difiere de *Calliostoma bravardi* Borchert, 1901, por ser ésta de menor tamaño, tener solo ocho cordones concéntricos planos en el último anfracto y 13 cordones concéntricos en la base; callo umbilical mucho menos desarrollado. Difiere de *Calliostoma doellojuradoi* Carral Tolosa, 1942, por tener ésta vueltas planas, la última angulosa, con 12 cordones lisos y finos y con cordones granulosos en las primeras vueltas. Difiere de *Calliostoma bonaerensis* Carral Tolosa, 1942, por tener ésta surcos suturales profundos de los que sobresalen dos cordones lisos; cordones espirales granulosos en la primera vuelta y lisos y granulosos en la penúltima vuelta. Difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones gruesos y lisos en la ultima vuelta, con dos cordones granulosos y en la penúltima dos cordones lisos, fuertes y un cordón granuloso. Difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta seis

six granulose cords on the last whorl and from seven to nine smooth spiral ones on the base.

CALLIOSTOMA (CALLIOSTOMA) MEISTERI, n. sp.
Plate 2, figure 7

Description: Shell small, turbiniform, not umbilicate; four and one-half whorls. Suture marked by one fine, deep groove; peristome slightly angulate and mouth subquadrate. Columella concave and short, with two small longitudinal plaits. Ornamentation on the last whorl consisting of one strong smooth cord, giving an angulosity to the whorl, followed by four well-spaced granulose cords. The penultimate whorl has two smooth cords, the basal wider than the next, and three granulose cords, all widely spaced. Base with six wide flat cords, especially the middle two.

Holotype: MPEF-PI-095; total height: 6.5 mm; last whorl: width 6.6 mm, height 2.8 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the geologist Lic. Carlos Meister of the Centro Nacional Patagónico (CENPAT) of Puerto Madryn.

Discussion: Calliostoma meisteri, n. sp., differs from *Calliostoma punctatulum* Borchert, 1901, which has six granulose cords on the last whorl and five granulose ones on the penultimate; but on the base it has eight smooth convex cords and two granulose periumbilical ones. *Calliostoma bravardi* Borchert, 1901, differs in having eight smooth flat cords on the last whorl and 13 smooth heavy ones on the base. *Calliostoma puelchanum* Borchert, 1901, has three heavy well-spaced cords and two granulose cords on the last whorl; the base has seven to nine flat cords. *Calliostoma doellojuradoi* Carral Tolosa, 1942, has 12 smooth fine cords on the last whorl, and on the early whorls, granulose ones. It also differs from *Calliostoma bonaerensis* Carral Tolosa, 1942, which has the whorls separated by deep grooves, in which there are two smooth cords; it has on the first whorl six granulose cords but on the second it has three granulose ones, with three fine smooth cords intercalated. It cannot be compared with *Calliostoma lepidum* (Philippi, 1893).

cordones granulosos en el último anfracto y de siete a nueve cordones lisos, concéntricos en la base.

CALLIOSTOMA (CALLIOSTOMA) MEISTERI, n. sp.
Lámina 2, figura 7

Descripción: Concha pequeña, turbiniforme, no umbilicada; cuatro y medio anfractos. Suturas marcadas por un fino y profundo surco; peristoma poco anguloso y boca subcuadrada. Columela cóncava y corta, con dos pequeños pliegues longitudinales. Ornamentación del último anfracto constituída por un fuerte y liso cordón que da angulosidad al anfracto, al que siguen cuatro cordones granulosos, muy espaciados entre si. El penúltimo anfracto consta de dos cordones lisos, el basal más ancho que el siguiente y tres cordones granulosos, todos ampliamente espaciados. Base con seis cordones anchos y planos, especialmente los dos del medio.

Holotipo: MPEF-PI-095; altura total: 6,5 mm; último anfracto: ancho 6,6 mm, altura 2,8 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geólogo Lic. Carlos Meister del Centro Nacional Patagónico (CENPAT) de Puerto Madryn.

Discusión: Calliostoma meisteri, n. sp., difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta seis cordones granulosos en la última vuelta y cinco granulosos en la penúltima; mientras que en la base posee ocho cordones liso convexos y dos granulosos periumbilicales. Difiere de *Calliostoma bravardi* Borchert; 1901, por tener ésta ocho cordones lisos y planos en el último anfracto y 13 cordones lisos y gruesos en la base. Difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones gruesos y espaciados y dos cordones granulosos en el último anfracto; la base con siete a nueve cordones planos. Difiere de *Calliostoma doellojuradoi* Carral Tolosa, 1942, por tener ésta 12 cordones lisos y finos en la última vuelta, y en las primeras vueltas, cordones granulosos. También difiere de *Calliostoma bonaerensis* Carral Tolosa, 1942, por tener ésta anfractos separados por surcos profundos de los que sobresalen dos cordones lisos; tener en la primera vuelta seis cordones granulosos mientras que en la segunda tiene tres cordones granulosos, con tres finos, lisos intercalados. No es comparable con *Calliostoma lepidum* (Philippi, 1893).

CALLIOSTOMA (CALLIOSTOMA) TROMBOTTOI, n. sp.
Plate 2, figure 8

Description: Shell small, low, whorls very convex; not umbilicate. Aperture slightly angulate, almost oval. Columella convex with strong depression directed toward the umbilicus. Ornamentation on the last whorl consisting of six heavy convex slightly projecting cords; penultimate whorl with five heavy convex cords. Base with six low heavy convex cords.

Holotype: MPEF-PI-096; total height: 4 mm; last whorl: width 6 mm, height 3 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the geologist Dr. Dario Trombotto, of the Centro Nacional Patagónico (CENPAT) of Puerto Madryn.

Discussion: Calliostoma trombottoi, n. sp., differs from *Calliostoma puelchanum* Borchert, 1901, which has three heavy well-separated smooth cords and two granulose ones on the last whorl. *Calliostoma punctatulum* Borchert, 1901, has a much higher shell and six granulose cords on the last whorl. *Calliostoma bravardi* Borchert, 1901, has a more conical shell, being ornamented on the last whorl with eight smooth flat cords and having 13 smooth cords on the base.

CALLIOSTOMA (CALLIOSTOMA) TROMBOTTOI, n. sp.
Lámina 2, figura 8

Descripción: Concha pequeña, baja, de vueltas muy convexas; no umbilicada. Abertura poco angulada, casi oval. Columela convexa con fuerte retracción hacia el ombligo. Ornamentación del último anfracto constituída por seis gruesos cordones convexos y poco salientes; penúltimo anfracto con cinco cordones gruesos y convexos. Base con seis cordones gruesos y convexos, bajos.

Holotipo: MPEF-PI-096: altura total: 4 mm; último anfracto: ancho 6 mm, altura 3 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geólogo Dr. Dario Trombotto, del Centro Nacional Patagónico (CENPAT), de Puerto Madryn.

Discusión: Calliostoma trombottoi, n. sp., difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones lisos y gruesos, bien separados y dos cordones granulosos en el último anfracto. Difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta concha mucho más alta y seis cordones granulosos en el último anfracto. De *Calliostoma bravardi* Borchert, 1901, difiere por tener ésta concha más cónica, estar ornamentado el último anfracto con ocho cordones lisos y planos y tener 13 cordones lisos en la base.

CALLIOSTOMA (CALLIOSTOMA) ARGENTINUM, n. sp.
Plate 2, figure 9

Description: Shell small, turbinate; five and one-half angulate whorls, the last biangulate; suture slightly defined; peristome biangulate; base slightly convex; columella concave, with a small oblique fold; not umbilicate. Ornamentation on the last whorl formed by one fine, smooth cord, one very fine cord, one heavy and smooth cord, one fine and smooth cord; it is followed by one heavy angulate cord, forming the shoulder of the whorl, and two finer granulose cords. On the penultimate whorl, only one very fine smooth basal cord and three granulose cords, similar to those of the previous whorl. Base with eight fine smooth cords.

Holotype: MPEF-PI-097; total height: 6 mm; last whorl: width 6 mm, height 2.6 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the Argentine Republic.

Discussion: Calliostoma argentinum, n. sp., differs from *Calliostoma punctatulum*

CALLIOSTOMA (CALLIOSTOMA) ARGENTINUM, n. sp.
Lámina 2, figura 9

Descripción: Concha pequeña, turbinada; cinco y medio anfractos, angulosos, la última biangulada; suturas poco definidas; peristoma biangulado; base poco convexa; columela cóncava, con pequeño repliegue oblicuo; no umbilicada. Ornamentación del último anfracto formada por un cordón fino y liso, uno muy fino, uno grueso y liso, uno fino y liso; se continúa con uno grueso y anguloso que forma el hombro del anfracto y dos más finos también granulosos. En el penúltimo anfracto, solo hay un cordón basal muy fino y liso, uno grueso y liso y tres cordones granulosos, similares a los del anfracto anterior. Base con ocho cordones finos y lisos.

Holotipo: MPEF-PI-097; altura total: 6 mm; último anfracto: ancho 6 mm, altura 2,6 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado a la República Argentina.

Discusión: Calliostoma argentinum, n. sp., difiere de *Calliostoma punctatulum*

Borchert, 1901, which has on the last whorl six granulose cords, with fine intermediary granulose ones. Base with seven smooth flat cords, lacking an angulation on the whorls. *Calliostoma puelchanum* Borchert, 1901, differs in having three heavy well-spaced smooth cords, two more granulose cords on the last whorl and, on the penultimate whorl, five granulose cords, without the fine intermediary ones; the base with eight convex smooth cords and two granulose periumbilical ones. *Calliostoma bravardi* Borchert, 1901, has eight smooth flat cords on the last whorl and 13 smooth heavy cords on the base. *Calliostoma doellojuradoi* Carral Tolosa, 1942, has 12 smooth fine cords on the last whorl and on the earlier whorls, granulose ones. *Calliostoma bonaerensis* Carral Tolosa, 1942, has the whorls separated by grooves, in which there are two smooth cords; on the last whorl six granulose spiral cords and on the penultimate whorl three granulose cords, intercalated with three finer smooth ones.

Calliostoma (Calliostoma) fidalgoi, n. sp.
Plate 2, figure 10

Description: Shell small, turbiniform, not umbilicate; five and one-half whorls approximately (apex broken); whorls convex; peristome angulate, mouth subquadrate; columella almost straight, with a slight fold. Ornamentation on the last whorl formed by two heavy convex cords, followed by three granulose cords. On the penultimate whorl the sequence is repeated. Base with eight flat cords, the fifth and sixth, counting from the periphery, are wider.

Holotype: MPEF-PI-098; total height: 6 mm; last whorl: width 5 mm, height 1.9 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the Argentinian geologist Dr. Francisco Fidalgo.

Discussion: Calliostoma fidalgoi, n. sp., differs from *Calliostoma puelchanum* Borchert, 1901, which has three very heavy smooth cords and two granulose ones on the last whorl; on the penultimate whorl only two heavy smooth cords and one granulose one. *Calliostoma punctatulum* Borchert, 1901, differs in having an ornamentation consisting of six granulose cords

Borchert, 1901, por tener ésta en la última vuelta seis cordones granulosos, con finos cordones granulosos intermedios. Base con siete cordones lisos y planos y ausencia de angulación en los anfractos. Difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres gruesos cordones lisos y espaciados, más dos granulosos en el último anfracto y cinco granulosos, sin los finos intermedios en el penúltimo anfracto; la base con ocho cordones lisos, convexos y dos granulosos, periumbilicales. Difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta ocho cordones lisos y planos en el último anfracto y 13 cordones lisos y gruesos en la base. Difiere de *Calliostoma doellojuradoi* Carral Tolosa, 1942, por tener ésta 12 cordones lisos y finos en la última vuelta y en las primeras, cordones granulosos. Difiere de *Calliostoma bonaerensis* Carral Tolosa, 1942, por tener ésta anfractos separados por surcos de los que sobresalen dos cordones lisos; en la última vuelta seis cordones espirales granulosos y en la penúltima vuelta tres granulosos, intercalados con tres lisos más finos.

Calliostoma (Calliostoma) fidalgoi, n. sp.
Lámina 2, figura 10

Descripción: Concha pequeña, turbiniforme, no umbilicada; cinco y medio anfractos aproximadamente (ápice roto); anfractos convexos; peristoma anguloso, boca subcuadrada; columela casi recta, con leve repliegue. Ornamentación del último anfracto formada por dos cordones gruesos y convexos, a los que les siguen tres cordones granulosos. En la penúltima vuelta se repite esta secuencia. Base con ocho cordones planos, el quinto y sexto, contando desde la periferia, son anchos.

Holotipo: MPEF-PI-098; altura total: 6 mm; último anfracto: ancho 5 mm, altura 1,9 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geólogo argentino Dr. Francisco Fidalgo.

Discusión: Calliostoma fidalgoi, n. sp., difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones muy gruesos y lisos y dos granulosos en el último anfracto; en la penúltima vuelta tiene solo dos cordones gruesos y lisos y un solo cordón granuloso. Difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta su ornamentación constituída por seis cordones granulosos y uno fino

and one fine basal one, but on the penultimate whorl it has five granulose cords. *Calliostoma bravardi* Borchert, 1901, has eight flat smooth cords on the last whorl, separated by deep grooves. Also it differs from *Calliostoma lepidum* (Phillipi, 1893), which has three smooth cords, and one granulose one on the last whorl.

Calliostoma (Calliostoma) caminosi, n. sp.
Plate 2, figure 11

Description: Shell conical but very flat, three and one-half whorls, non-umbilicate; whorls flat, slightly differentiated; peristome very angulate, mouth subquadrate; columella convex with umbilical fold on which may be seen two plaits and one basal denticule. Base slightly convex, with the last whorl angulate. Ornamentation of the last whorl consisting of one heavy double smooth cord, followed by four double smooth cords. Base with 16 fine flat cords.

Holotype: MPEF-PI-099; total height: 5 mm; last whorl: width 6 mm, height 2.2 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the geologist Dr. Roberto Caminos.

Discussion: Calliostoma caminosi, n. sp., differs from *Calliostoma bravardi* Borchert, 1901, which has more convex whorls, ornamentation formed by eight smooth cords on the last whorl and 13 smooth spiral ones on the base. *Calliostoma doellojuradoi* Carral Tolosa, 1942, differs in having 12 fine smooth cords on the last whorl, and on the earlier whorls the initial cords with granulations. *Calliostoma bonaerensis* Carral Tolosa, 1942, has sutural grooves, in which there are two smooth cords; it has six spiral cords with small nodules on the first whorl whorl and the base with heavy cords between which are intercalated finer ones. *Calliostoma punctatulum* Borchert, 1901, differs in having only six granulose cords, between which are intercalated other finer ones, also granulose.

Calliostoma (Calliostoma) bonorinoi, n. sp.
Plate 2, figure 12

basal, mientras que en la penúltima vuelta tiene cinco cordones granulosos. Difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta ocho cordones lisos y planos en la última vuelta, separados por surcos profundos. También difiere de *Calliostoma lepidum* (Phillipi, 1893), por tener ésta tres cordones lisos y uno granuloso en la ultima vuelta.

Calliostoma (Calliostoma) caminosi, n. sp.
Lámina 2, figura 11

Descripción: Concha cónica pero muy plana, tres y medio vueltas, anónfala; anfractos planos, poco diferenciados; peristoma muy anguloso, boca subcuadrada; columela convexa con repliegue umbilical en el que se observan dos pliegues y un denticulo final. Base poco convexa, con el último anfracto anguloso. Ornamentación del último anfracto constituída por un grueso y doble cordón liso al que le siguen cuatro cordones dobles, lisos. Base con 16 cordones finos y planos.

Holotipo: MPEF-PI-099; altura total: 5 mm; último anfracto: ancho 6 mm, altura 2,2 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geólogo Dr. Roberto Caminos.

Discusión: Calliostoma caminosi, n. sp., difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta vueltas más convexas, ornamentación formada por ocho cordones lisos en la última vuelta y 13 cordones lisos, concéntricos en la base. Difiere de *Calliostoma doellojuradoi* Carral Tolosa, 1942, por tener ésta 12 cordones lisos y finos en la última vuelta, y en las primeras vueltas, los cordones iniciales con granulación. Difiere de *Calliostoma bonaerensis* Carral Tolosa, 1942, por tener ésta surcos suturales de los que sobresalen dos cordones lisos, tener seis cordones espirales con nudos pequeños en la primera vuelta y base con cordones gruesos entre los que se intercalan otros más finos. Difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta solo cordones granulosos en número de seis, entre los que se intercalan algunos más finos, también granulosos.

Calliostoma (Calliostoma) bonorinoi, n. sp.
Lámina 2, figura 12

Description: Shell small, turbiniform, whorls convex, the last angulate, well differentiated; without umbilicus. Aperture angulate, subquadrate; columella straight and wide, with fine edge that begins at the umbilical zone. Ornamentation on the last whorl consisting of one heavy smooth cord, one fine smooth cord, one very fine smooth cord and three granulose cords, with one very fine one between the second and third and another very fine subsutural one. The penultimate whorl has one smooth heavy cord, one fine smooth cord, one very fine smooth one, three granulose ones and one very fine smooth subsutural one. Base with five flat cords and two convex periumbilical ones.

Holotype: MPEF-PI-100; total height: 6 mm; last whorl: width 6.7 mm, height 3 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the geologist Dr. Felix Gonzalez Bonorino.

Discussion: Calliostoma bonorinoi, n. sp., differs from *Calliostoma punctatulum* Borchert, 1901, which has as ornament only granulose cords, which have intercalated fine cords also granulose and, on the base, eight convex smooth cords and two granulose ones. *Calliostoma puelchanum* Borchert, 1901, has three very heavy cords and two fine granulose ones on the last whorl; lacking the columellar costellation. *Calliostoma bravardi* Borchert, 1901, has 13 heavy smooth spiral cords on the base and on the whorls, only smooth flat cords. It is not comparable to *Calliostoma lepidum* (Philippi, 1893), or *Calliostoma doellojuradoi* Carral Tolosa, 1942.

Descripción: Concha pequeña, turbiniforme, anfractos convexos, el último anguloso, bien diferenciados; sin ombligo. Abertura angulosa, subcuadrada; columela recta y ancha, con fina arista que nace de la zona umbilical. Ornamentación del último anfracto constituída por un cordón grueso y liso, uno fino y liso, uno muy fino, liso y tres cordones granulosos, con uno muy fino entre el segundo y el tercero y otro muy fino subsutural. El penúltimo anfracto consta de un cordón liso y grueso, uno fino y liso, uno muy fino y liso, tres granulosos y uno muy fino liso subsutural. Base con cinco cordones planos y dos convexos periumbilicales.

Holotipo: MPEF-PI-100; altura total: 6 mm; último anfracto: ancho 6,7 mm, altura 3 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geólogo Dr. Félix González Bonorino.

Discusión: Calliostoma bonorinoi, n. sp., difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta como ornamento solo cordones granulosos, que llevan intercalados finos cordones también granulosos y por tener en su base ocho cordones lisos, convexos y dos granulosos. Difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones muy gruesos y dos granulosos finos en el último anfracto; está ausente la costulación columelar. Difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta 13 cordones concéntricos lisos y gruesos en la base y en las vueltas, solo cordones lisos y planos. No es comparable con *Calliostoma lepidum* (Philippi, 1893), ni con *Calliostoma doellojuradoi* Carral Tolosa, 1942.

CALLIOSTOMA (CALLIOSTOMA) NULLOI, n. sp.
Plate 2, figure 13

Description: Shell small, coniform, whorls almost flat, slightly differentiated, the last angulate; not umbilicate. Columella strong and barely concave, with umbilical callus; aperture angulate and subtriangular. Ornamentation on last whorl consisting of one double smooth basal cord, followed by four fine well-spaced smooth cords; between the first and second and between the third and fourth, one very fine smooth cord. The penultimate whorl beginning with one double smooth cord and three single well-spaced smooth cords, lacking the very fine intermediary cords. Base with 14 cords, those nearer the margin, heavy and smooth, the others fine and smooth.

Holotype: MPEF-PI-101; height: 4 mm (apex broken); last whorl: width 6.2 mm, height 2 mm.

CALLIOSTOMA (CALLIOSTOMA) NULLOI, n. sp.
Lámina 2, figura 13

Descripción: Concha pequeña, coniforme, anfractos casi planos, poco diferenciados, el último anguloso; no umbilicada. Columela fuerte y apenas cóncava, con callo umbilical; abertura angulosa y subtriangular. Ornamentación del último anfracto constituída por un cordón basal doble y liso, al que le siguen cuatro cordones finos y lisos, muy espaciados; entre el primero y el segundo y entre el tercero y el cuarto, corre un finísimo cordón liso. El penúltimo anfracto comienza con un cordon doble, liso y tres cordones simples, lisos y muy espaciados, faltando los muy finos cordones intermedios. Base con 14 cordones, el más cercano al borde, grueso y liso, los demás finos y lisos.

Holotipo: MPEF-PI-101; altura: 4 mm (ápice roto); último anfracto: ancho 6,2 mm, altura 2 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the geologist Dr. Francisco Nullo.

Discussion: Calliostoma nulloi, n. sp., differs from *Calliostoma puelchanum* Borchert, 1901, which has three heavy smooth cords and two granulose ones on the last whorl. *Calliostoma bravardi* Borchert, 1901, has eight smooth spiral cords on the last whorl. It is not comparable to *Calliostoma lepidum* (Philippi, 1893), *Calliostoma bonaerensis* Carral Tolosa, 1942, or *Calliostoma doellojuradoi* Carral Tolosa, 1942.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geólogo Dr. Francisco Nullo.

Discusión: Calliostoma nulloi, n. sp., difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones gruesos y lisos y dos cordones granulosos en el último anfracto. Difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta ocho cordones lisos, concéntricos en el último anfracto. No es comparable con *Calliostoma lepidum* (Philippi, 1893), con *Calliostoma bonaerensis* Carral Tolosa, 1942, ni con *Calliostoma doellojuradoi* Carral Tolosa, 1942.

Calliostoma (Calliostoma) castellanosae, n. sp.

Plate 2, figure 14

Description: Shell turbiniform, very high, seven and one-half convex whorls, barely noticable due to shallowness of suture, the last not angulate; base convex, non-umbilicate. Peristome somewhat angulate; columella almost straight, with vertical denticle. Ornamentation on the last whorl consisting of 12 granulose cords, heavy and fine ones alternating, reduced to eight on the preceding whorls and to six on the earliest whorls. The two last whorls have the lower cord within the suture. Base with eight smooth cords and six granulose periumbilical ones.

Holotype: MPEF-PI-102; total height: 16 mm; last whorl: width 12.1 mm, height 5 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the malacologist Dra. Zulma A. de Castellanos.

Calliostoma (Calliostoma) castellanosae, n. sp.

Lámina 2, figura 14

Descripción: Concha turbiniforme, muy alta, siete y medio anfractos convexos, anfractos poco notorios por la escasa profundidad de las suturas, el último no anguloso; base convexa, anónfala. Peristoma poco angulado; columela casi recta, con dentículo vertical. Ornamentación del último anfracto constituída por 12 cordones granulosos, entre gruesos y finos intercalados, que se reducen a ocho en los anfractos siguientes y a seis en las vueltas primeras. Las dos últimas vueltas presentan el cordón inferior metido en la sutura. Base con ocho cordones lisos y seis periumbilicales granulosos.

Holotipo: MPEF-PI-102; altura total: 16 mm; último anfracto: ancho 12,1 mm, altura 5 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado a la malacóloga Dra. Zulma A. de Castellanos.

Discussion: Calliostoma castellanosae, n. sp., differs from *Calliostoma punctatulum* Borchert, 1901, by the lack of the perimetral angulation, by the more convex whorls, its greater height, as well as by the ornamentation, which in the latter species has only six granulose cords on the last whorl and on the base from seven to nine smooth spiral cords. *Calliostoma bravardi* Borchert, 1901, is ornamented by eight smooth flat cords, with the aperture more quadrangular. *Calliostoma doellojuradoi* Carral Tolosa, 1942, differs in having a perimetral angulosity on the last whorl and is ornamented with 12 fine smooth cords on

Discusión: Calliostoma castellanosae, n. sp., difiere de *Calliostoma punctatulum* Borchert, 1901, por la ausencia de angulación perimetral, por sus anfractos más convexos, su mayor altura, asi como también por su ornamentación, ya que esta última especie tiene solo seis cordones granulosos en el último anfracto y en su base de siete a nueve cordones concéntricos lisos. Difiere de *Calliostoma bravardi* Borchert, 1901, por estar ésta ornamentada con ocho cordones lisos y planos, con una abertura más cuadrangular. Difiere de *Calliostoma doellojuradoi* Carral Tolosa, 1942, en que ésta tiene angulosidad perimetral en el último anfracto y estar ornamentado con 12 cordones finos y lisos en la última vuelta. Respecto a *Calliostoma bonaerensis* Carral

the last whorl. *Calliostoma bonaerensis* Carral Tolosa, 1942, has sutural grooves, in which there are two smooth cords, and has only six granulose cords. It is not comparable to *Calliostoma lepidum* (Philippi, 1893), or *Calliostoma puelchanum* Borchert, 1901.

Calliostoma (Calliostoma) mapuchei, n. sp.
Plate 2, figure 15

Description: Shell turbiniform, very broad and slightly elevated, whorls convex, last whorl not angulate; sutural line poorly marked; peristome somewhat angulate; aperture subquadrate; base convex, without umbilicus. Columella very concave, strong umbilical callus with one plait. Ornamentation on the last whorl consisting of 12 fine flat cords, between which are intercalated very fine cords only visible with a microscope; on the penultimate whorl eight fine flat cords, with a few very fine ones intercalated. The spaces between the cords are twice the width of the cords. Base with 14 to 16 flat cords. Visible on the whorls are oblique growth lines that extend to the umbilical zone.

Holotype: MPEF-PI-103; total height: 12 mm; last whorl: width 16 mm, height 6.5 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the Mapuche tribe of Chubut Province.

Discussion: Calliostoma mapuchei, n. sp., differs from *Calliostoma bravardi* Borchert, 1901, which has the shell more elevated and pointed, with heavier cords, and which lacks the umbilical callus. *Calliostoma doellojuradoi* Carral Tolosa, 1942, has granulose cords on the early whorls, an angulosity on the last whorl, and is flat. It is not comparable to *Calliostoma punctatulum* Borchert, 1901, *Calliostoma puelchanum* Borchert, 1901, or *Calliostoma lepidum* (Philippi, 1893).

Calliostoma (Calliostoma) ameghinoi, n. sp.
Plate 2, figure 16

Description: Shell turbinate, imperforate, with four and one-half convex whorls; suture poorly delimited; last whorl slightly angulate; base convex; aperture subquadrate; columella weakly concave, with a slight protrusion toward the aperture, terminating in a smooth fold directed outward. Ornamentation on the last whorl consisting of three rounded heavy smooth

Tolosa, 1942, difiere por tener ésta surcos suturales de los que sobresalen dos cordones lisos y por tener solo seis cordones granulosos. No es comparable con *Calliostoma lepidum* (Philippi, 1893), ni con *Calliostoma puelchanum* Borchert, 1901.

Calliostoma (Calliostoma) mapuchei, n. sp.
Lámina 2, figura 15

Descripción: Concha turbiniforme, muy ancha y poco elevada, anfractos convexos, última vuelta no angulosa; línea sutural poco marcada; peristoma poco anguloso; abertura subcuadrada; base convexa, sin ombligo. Columela muy cóncava, fuerte callo umbilical con un pliegue. Ornamentación del último anfracto constituída por 12 cordones finos y planos, entre los que se intercalan muy finos cordones solo visibles al microscopio; en el penúltimo anfracto se cuentan ocho cordones finos y planos, con muy pocos cordones muy finos intercalados. Los espacios entre los cordones son el doble del ancho de ellos. Base con 14 a 16 cordones planos. Son visibles en los anfractos lineas de crecimiento oblicuas que se prolongan hasta la zona umbilical.

Holotipo: MPEF-PI-103; altura total: 12 mm; último anfracto: ancho 16 mm, altura 6,5 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado a la tribu Mapuche de la Provincia del Chubut.

Discusión: Calliostoma mapuchei, n. sp., difiere de *Calliostoma bravardi* Borchert, 1901, por tener ésta concha más elevada y aguda, por sus cordones más gruesos, y por la ausencia de callo umbilical. Difiere de *Calliostoma doellojuradoi* Carral Tolosa, 1942, por tener ésta en las primeras vueltas cordones granulosos, por la angulosidad de la última vuelta y por ser ésta plana. No es comparable con *Calliostoma punctatulum* Borchert, 1901, con *Calliostoma puelchanum* Borchert, 1901, ni con *Calliostoma lepidum* (Philippi, 1893).

Calliostoma (Calliostoma) ameghinoi, n. sp.
Lámina 2, figura 16

Descripción: Concha turbinada, imperforada, con cuatro y medio anfractos convexos; sutura poco delimitada; último anfracto poco anguloso; base convexa; abertura subcuadrada; columela debilmente concava, con leve protrución hacia la apertura, terminando en un suave repliegue hacia afuera. Ornamentación del último anfracto constituída por tres cordones concén-

spiral cords, followed by two finer smooth ones, then five granulose spiral cords. On the penultimate whorl, the same ornamentation. Base circular with 12 to 14 fine smooth cords.

Holotype: MPEF-PI-104; total height: 9.5 mm; last whorl: width 10.5 mm, height 3.2 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to Dr. Carlos Ameghino.

Discussion: Calliostoma ameghinoi, n. sp., differs from *Calliostoma punctatulum* Borchert, 1901, which has five smooth cords on the last whorl, which are repeated in the others, and by the number of basal cords (seven to nine). *Calliostoma puelchanum* Borchert, 1901, differs in having three heavy smooth cords, with a fine one intercalated and only one granulose one; and the base with seven to nine flat cords. *Calliostoma bravardi* Borchert, 1901, differs in having an ornamentation of eight flat cords and on the base 13 heavy smooth cords. *Calliostoma doellojuradoi* Carral Tolosa, 1942, has 12 flat smooth cords on the last whorl and 13 heavy smooth ones on the base. *Calliostoma bonaerensis* Carral Tolosa, 1942, has the suture in the form of a groove, in which there are two smooth cords, with six granulose cords on the first whorl with fine ones intercalated on the second.

CALLIOSTOMA (CALLIOSTOMA) PUNCTATULUM Borchert, 1901
Plate 2, figure 17

Description: Shell turbiniform, whorls somewhat convex, well defined, in spite of the slight differentiation of the suture. Each whorl with six spiral granulose cords, between which are other finer ones, with granulations. Growth lines well marked on the base and slightly visible on the spire. Base slightly convex, forming with the last whorl a sharp angle. On the base nine smooth spiral cords, and intercalated between these, one fine smooth cord. Mouth rhombic. Columella concave with columellar callus.

Hypotype: MPEF-PI-105; total height: 8 mm; last whorl: width 6.5 mm, height 2 mm.

Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Discussion: Reported here for the first time from the Entrerriense Formation of

tricos, redondeados, gruesos y lisos, a los que le siguen dos más finos y lisos, continúa con cinco cordones concéntricos granulosos. En la penúltima vuelta, se observa idéntica ornamentación. Base circular con 12 a 14 cordones finos y lisos.

Holotipo: MPEF-PI-104; altura total: 9,5 mm; último anfracto: ancho 10,5 mm, altura 3,2 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al Dr. Carlos Ameghino.

Discusión: Calliostoma ameghinoi, n. sp., difiere de *Calliostoma punctatulum* Borchert, 1901, por tener ésta cinco cordones lisos en el último anfracto, que se repiten en los demás, por la cantidad de cordones basales (siete a nueve). Difiere de *Calliostoma puelchanum* Borchert, 1901, por tener ésta tres cordones gruesos y lisos, con un fino intercalado y un solo cordón granuloso; la base con siete a nueve cordones planos. Respecto a *Calliostoma bravardi* Borchert, 1901, difiere por tener ésta una ornamentación de cordones planos en número de ocho y en la base 13 cordones lisos y gruesos. Difiere de *Calliostoma doellojuradoi* Carral Tolosa, 1942, por tener ésta 12 cordones lisos y planos en el último anfracto y 13 cordones lisos y gruesos en la base. Difiere de *Calliostoma bonaerensis* Carral Tolosa, 1942, por tener ésta suturas en forma de surcos de los que sobresalen dos cordones lisos, con seis cordones granulosos en la primera vuelta, con finos intercalados en la segunda.

CALLIOSTOMA (CALLIOSTOMA) PUNCTATULUM Borchert, 1901
Lámina 2, figura 17

Descripción: Concha turbiniforme, anfractos algo convexos, bien definidos a pesar de la poca diferenciación de las suturas. Cada vuelta posee cordones concéntricos granulosos en número de seis, entre los cuales se observan otros, más finos, con granulaciones. Lineas de crecimiento bien notorias en la base y poco visibles en la espira. Base apenas convexa, formando con la última vuelta un ángulo agudo. En la base se cuentan nueve cordones concéntricos lisos, e intercalandose entre ellos, un fino cordón liso. Boca rómbica. Columela cóncava con callo columelar.

Hipotipo: MPEF-PI-105; altura total: 8 mm; último anfracto: ancho 6,5 mm, altura 2 mm.

Localidad: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Discusión: Se describe por primera vez para la Formación Entrerriense de la Pro-

Chubut Province is the species *Calliostoma punctatulum* Borchert, 1901, the holotype of which comes from Paraná (Entre Rios). The examples obtained at Baliza Punta Flecha present no marked differences from the example of Borchert; but some of our specimens show on the base two granulose pericolumellar cords and the columella is practically straight.

Subgenus FENEONIANA Kolesnikov, 1939

CALLIOSTOMA (FENEONIANA) STIPANICICI, n. sp.

Plate 2, figure 18

Description: Shell with trocoid appearance; thin, imperforate, with fine sculpture. Four and one-half whorls plus the nepionic ones. Spire moderately elevated, whorls convex. Aperture subtriangular. Outer lip simple, smoothly crenulate and strongly angulate. Basal lip slightly carinate. Columella somewhat arcuate and thick. Beginning near the umbilical area a fine rib that ends in a strong curve, forming a groove with the terminal part of the columella. The spiral sculpture of the body whorl consists of a sharp peripheral carina and 12 flat spiral cords, equal in thickness; the grooves between the cords are very fine. All of the surface crossed by very visible growth lines. The base is conical, with one strong peripheral cord and six finer one, with very fine cords alternating with them. Shell not umbilicate, with strong growth lines on the base.

Holotype: MPEF-PI-139; height: 5 mm; width: 3 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the geologist Dr. Pedro Stipanicic.

Discussion: It has been impossible for us to obtain a good description of the holotype of *Calliostoma (Feneoniana) feneonianus* (d'Orbigny, 1845), for this reason the fossil species is tentatively described as a new species, inasmuch as the subgenus *Feneoniana* Kolesnikov, 1939, is reported for the first time in this work from the Entrerriense Formation of South America and for the Tertiary of Patagonia.

Family TURBINIDAE
Subfamily LIOTIINAE
Genus LIOTIA Gray, 1842

LIOTIA TERUGGII, n. sp.

Plate 4, figure 1

vincia del Chubut la especie *Calliostoma punctatulum* Borchert, 1901, cuyo holotipo procede de Paraná (Entre Rios). Los ejemplares obtenidos en Baliza Punta Flecha no presentan marcadas diferencias con el ejemplar de Borchert; pero algunos de nuestros especímenes muestran en la base dos cordones granulosos pericolumelares y la columela practicamente recta.

Subgénero FENEONIANA Kolesnikov, 1939

CALLIOSTOMA (FENEONIANA) STIPANICICI, n. sp.

Lámina 2, figura 18

Descripción: Concha de aspecto trocoide, delgada, imperforada y con fina escultura. Cuatro y media vueltas más las nepiónicas. Espira moderadamente elevada, vueltas convexas. Abertura subtriangular. Labio externo simple, suavemente crenulado y fuertemente angulado. Labio basal ligeramente carenado. Columela algo arqueada y gruesa. Cerca del area umbilical nace una fina costilla que termina en una fuerte curvatura, formando un surco con la parte terminal de la columela. La escultura espiral del habitáculo consiste en una aguda carena periférica y 12 cordones espirales, planos e iguales en espesor; los surcos entre los cordones son muy finos. Toda la superficie es cruzada por lineas de crecimiento muy visibles. La base es cónica, con un fuerte cordón periférico y seis mas finos, con muy finos cordones que se alternan con estos. Concha no umbilicada, con fuertes estrias de crecimiento en la base.

Holotipo: MPEF-PI-139; altura: 5 mm; ancho: 3 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geólogo Dr. Pedro Stipanicic.

Discusión: Nos ha sido imposible obtener una buena descripción del holotipo *Calliostoma (Feneoniana) feneonianus* (d'Orbigny, 1845), por ésta razon la especie fósil es descrita tentativamente como una nueva especie, considerando que el subgénero *Feneoniana* Kolesnikov, 1939, es mencionado por primera vez en éste trabajo para la Formación Entrerriense de Sudamérica y para el Terciario de Patagonia.

Familia TURBINIDAE
Subfamilia LIOTIINAE
Género LIOTIA Gray, 1842

LIOTIA TERUGGII, n. sp.

Lámina 4, figura 1

Description: Shell small, strong, with four whorls; spire very small. Last whorl very wide, much wider than high. Suture shallow. Body whorl ornamented with eight strong spiral cords; the first forming the shoulder of the whorl. Between the suture and the shoulder there is a slightly concave area, with marked growth lines. Between the spiral cords, numerous finer axial cords which cross over the spirals, forming small tubercules. On the penultimate whorl only four spiral cords and fine, slightly visible axial cords. Aperture very wide and semi-circular, with strong columellar callus, forming a marked posterior angulation with the labrum at the point of the body whorl. Outer lip strongly crenulated by the projection of the spiral ribs. Umbilicus not very wide but very deep; a carina begins at the anterior angle of the columellar callus, penetrates into the umbilicus and runs parallel to the outer margin of the callus. In some examples the lower cord also penetrates into the umbilicus.

Holotype: MPEF-PI-164; height: 11 mm; width: 11 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the geologist Dr. Mario Teruggi.

Discussion: Liotia teruggii, n. sp., differs from *Liotia admirabilis* E.A. Smith, 1890, which has a better development of the axial ornamentation, a greater number of spiral cords and lacks the posterior angulation of the columellar callus. *Liotia cancellata* Gray, 1847, differs in having the umbilicus bordered by one granulose cord, the labrum less crenulated and the columellar callus slightly visible, without posterior angulation. *Liotia miniata* Dall, 1889, has the ornamentation on the body whorl of only one spiral cord and one granulose one at the level of the shoulder. *Liotia variabilis* Dall, 1889, has stronger axial ornamentation in the form of spinose cords and granulose cords. The genus *Liotia* Gray, 1842, is reported for the first time in this work from the Entrerriense Formation of South America.

Superfamily EPITONIOIDEA
Family EPITONIIDAE
Subfamily EPITONIINAE
Genus EPITONIUM Röding, 1798
Subgenus EPITONIUM s.s.

Descripción: Concha pequeña, fuerte, con cuatro vueltas; espira muy pequeña. Ultimo anfracto muy amplio, mucho más ancho que alto. Suturas poco profundas. Habitáculo ornamentado con ocho fuertes cordones concéntricos; el primero forma el hombro del anfracto. Entre la sutura y el hombro existe un area levemente cóncava, con marcadas estrias de crecimiento. Entre los cordones concéntricos se observan numerosos cordones axiales mas finos, que al pasar sobre los concéntricos forman pequeños tubérculos. En la penúltima vuelta solo se cuentan cuatro cordones concéntricos y los finos cordones axiales, poco notorios. Abertura muy amplia, semi-circular, con fuerte callo columelar, que forma una marcada angulación posterior con el labro a nivel del habitáculo. Labro fuertemente crenulado por la proyección de las costillas concéntricas. Ombligo mediano pero muy profundo; una carena que nace del ángulo anterior del callo columelar penetra en el ombligo y corre paralela al borde externo del callo. En algunos ejemplares el cordón inferior penetra también en el ombligo.

Holotipo: MPEF-PI-164; altura: 11 mm; ancho: 11 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geólogo Dr. Mario Teruggi.

Discusión: Liotia teruggii, n. sp., difiere de *Liotia admirabilis* E.A. Smith, 1890, por tener ésta mayor desarrollo de la ornamentación axial, mayor número de cordones concéntricos y ausencia de la angulación posterior del callo columelar. Difiere de *Liotia cancellata* Gray, 1847, por tener ésta el ombligo bordeado por un cordón granuloso, labro menos crenulado y callo columelar poco notorio, sin angulación posterior. Difiere de *Liotia miniata* Dall, 1889, por tener ésta como ornamentación del habitáculo un solo cordón concéntrico y un granuloso a nivel del hombro. Difiere de *Liotia variabilis* Dall, 1889, por tener ésta fuerte ornamentación axial en forma de cordones espinosos y cordones granulosos. El género *Liotia* Gray, 1842, es mencionado en este trabajo por primera vez para la Formación Entrerriense de Sudamérica.

Superfamilia EPITONIOIDEA
Familia EPITONIIDAE
Subfamilia EPITONIINAE
Género EPITONIUM Röding, 1798
Subgénero EPITONIUM s.s.

EPITONIUM (EPITONIUM) ALBIDUM (d'Orbigny, 1842)
Plate 3, figure 1

Description: Shell rather light in structure, imperforate; six and one-half moderately convex whorls, attached by the costae only. Spire high, forming an angle of 27 degrees. Aperture subcircular. Outer lip expanded and reflected. Parietal area narrow and attached to body whorl by costae. Columella not readily definable. Suture very deep on early whorls, less so on later whorls. Sculpture consisting of twelve blade-like costae on the body whorl, not angled at whorl shoulder. Microscopic sculpture consisting of extremely fine spiral threads. No basal ridge.

Hypotype: MPEF-PI-009; length: 11.5 mm; width: 5 mm.

Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Discussion: We can detect no marked differences between the fossil specimens and the living specimens from the western Atlantic Ocean. *Epitonium (Epitonium) albidum* (d'Orbigny, 1842) is reported for the first time for the Entrerriense Formation of South America.

EPITONIUM (EPITONIUM) ANGULATUM (Say, 1830)
Plate 3, figure 2

Description: Shell rather strong in structure, imperforate. Spire high. forming an angle of 26 degrees. Aperture subcircular, outer lip expanded and reflected. Parietal lip thick and attached to body whorl by the costae. Columella not defined. Suture deep. Sculpture consisting of nine blade-like costae strongly reflected backwards. At the whorl shoulder, costae expanded and forming strong angle. Costae of each whorl aligned with those on preceding whorl and fused at points of contact. Microscopic sculpture consisting of numerous spiral threads.

Hypotype: MPEF-PI-017; length: 11 mm; width: 4 mm.

Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Discussion: There are no outstanding differences between the fossil specimens and the specimens living in the western Atlantic Ocean. Some fossil specimens have the spire more extended, with strong angles at the whorl shoulder on all the costae. *Epitonium angulatum* (Say, 1830) is reported for the first time for the Entrerriense Formation of South America.

EPITONIUM (EPITONIUM) ALBIDUM (d'Orbigny, 1842)
Lámina 3, figura 1

Descripción: Concha más bien delgada en su estructura, imperforada; seis y media vueltas moderadamente convexas y unidas solo por las costillas. Espira alta, formando un ángulo de 27 grados. Abertura subcircular. Labio externo expandido y reflejado. Labio parietal estrecho y unido al habitáculo solo por las costillas. Columela debilmente definida. Suturas muy profundas en las primeras vueltas y menos en las últimas. La escultura consiste en 12 costillas laminares en el habitáculo, sin angulaciones en el hombro. La estructura microscópica consiste en estrias concéntricas sumamente finas. Sin costilla basal.

Hipotipo: MPEF-PI-009; altura: 11,5 mm; ancho: 5 mm.

Localidad: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Discusión: No hemos observado marcadas diferencias entre estos especímenes fósiles y los vivientes en la costa oeste del Océano Atlántico. Algunos especímenes fósiles tienen las costillas más bajas. *Epitonium (Epitonium) albidum* (d'Orbigny, 1842) se menciona por primera vez para la Formación Entrerriense de Sudamérica.

EPITONIUM (EPITONIUM) ANGULATUM (Say, 1830)
Lámina 3, figura 2

Descripción: Concha más bien fuerte en estructura, imperforada. Espira alta, formando un ángulo de 26 grados. Abertura subcircular, labio externo expandido y reflejado. Labio parietal grueso y unido al habitáculo por las costillas. Columela no definida. Suturas profundas. La escultura consiste en nueve costillas laminares fuertemente reflejadas hacia atrás. A nivel del hombro las costillas se expanden formando un fuerte ángulo. Las costillas de cada vuelta se alinean con las del anfracto anterior, soldándose en el punto de contacto. La estructura microscópica consiste en númerosas estrías espirales.

Hipotipo: MPEF-PI-017; altura: 11 mm; ancho: 4 mm.

Localidad: Puerto Pirámide. Península Valdés. Provincia del Chubut, Argentina.

Discusión: No hemos observado diferencias notorias entre estos especímenes fósiles y los vivientes en el oeste del Océano Atlántico. *Epitonium angulatum* (Say, 1830) se menciona por primera vez para la Formación Entrerriense de Sudamérica.

PLATE 3

Figure Page

1. EPITONIUM (EPITONIUM) ALBIDUM (d'Orbigny, 1842) 27
MPEF-PI-009 (holotype); length: 11.5 mm, width: 5 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
2. EPITONIUM (EPITONIUM) ANGULATUM (Say, 1830) 27
MPEF-PI-017 (hypotype); length: 11 mm; width: 4 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
3. EPITONIUM (EPITONIUM) HUMPHREYSII (Kiener, 1838) 30
MPEF-PI-059 (hypotype); length: 14.5 mm, width: 5.5 mm (broken).
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
4. EPITONIUM (EPITONIUM) LEPTOSOMUM, n. sp. 30
MPEF-PI-061 (holotype); length: 12.5 mm, width: 4 mm (the early whorls broken).
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
5. EPITONIUM (EPITONIUM) UNIFASCIATUM (Sowerby, 1844) 31
MPEF-PI-062 (hypotype); length: 13 mm; width: 5 mm (nuclear whorls broken).
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
6. EPITONIUM (EPITONIUM) CINGOLANII, n. sp. 31
MPEF-PI-063 (holotype); length: 11.5 mm, width: 4 mm (nuclear whorls broken).
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
7. EPITONIUM (EPITONIUM) VENOSUM (Sowerby, 1844) 32
MPEF-PI-064 (hypotype); length: 7.5 mm, width: 3.8 mm (early whorls broken).
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
8. EPITONIUM (EPITONIUM) GEORGETTINA (Kiener, 1839) 32
MPEF-PI-065 (hypotype); length: 9 mm; width: 4 mm.
Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.
9. EPITONIUM (ASPERISCALA) MULTISTRIATUM (Say, 1826) 33
MPEF-PI-069 (hypotype); length: 11.5 mm; width: 5 mm (nuclear whorls broken).
Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.
10. EPITONIUM (ASPERISCALA) TONNII, n. sp. 33
MPEF-PI-066 (holotype); length: 13 mm; width: 4.5 mm (nuclear whorls broken).
Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.
11. EPITONIUM (ASPERISCALA) aff. NOVANGLIAE (Couthouy, 1838) 34
MPEF-PI-067 (hypotype); length: 15.5 mm; width: 5 mm (nuclear whorls broken).
Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.
12. EPITONIUM (ASPERISCALA) CHUBUTINUM (Ihering, 1907) 35
MPEF-PI-068 (hypotype); length: 12 mm; 5 mm (only 2½ whorls).
Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.
13. EPITONIUM (ASPERISCALA) QUIROGAI, n. sp. 35
MPEF-PI-006 (holotype); length: 11 mm; width: 4.5 mm; height of last whorl: 3 mm.
Aperture: length 2 mm, width 1.4 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.
14. EPITONIUM (GYROSCALA) CIONEI, n. sp. 36
MPEF-PI-070 (holotype); length: 10.5 mm; width: 5 mm (nuclear whorls broken).
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
15. CYLINDRISCALA sp. 37
MPEF-PI-071 (hypotype); measurement impractical.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

(Continued on p. 30)

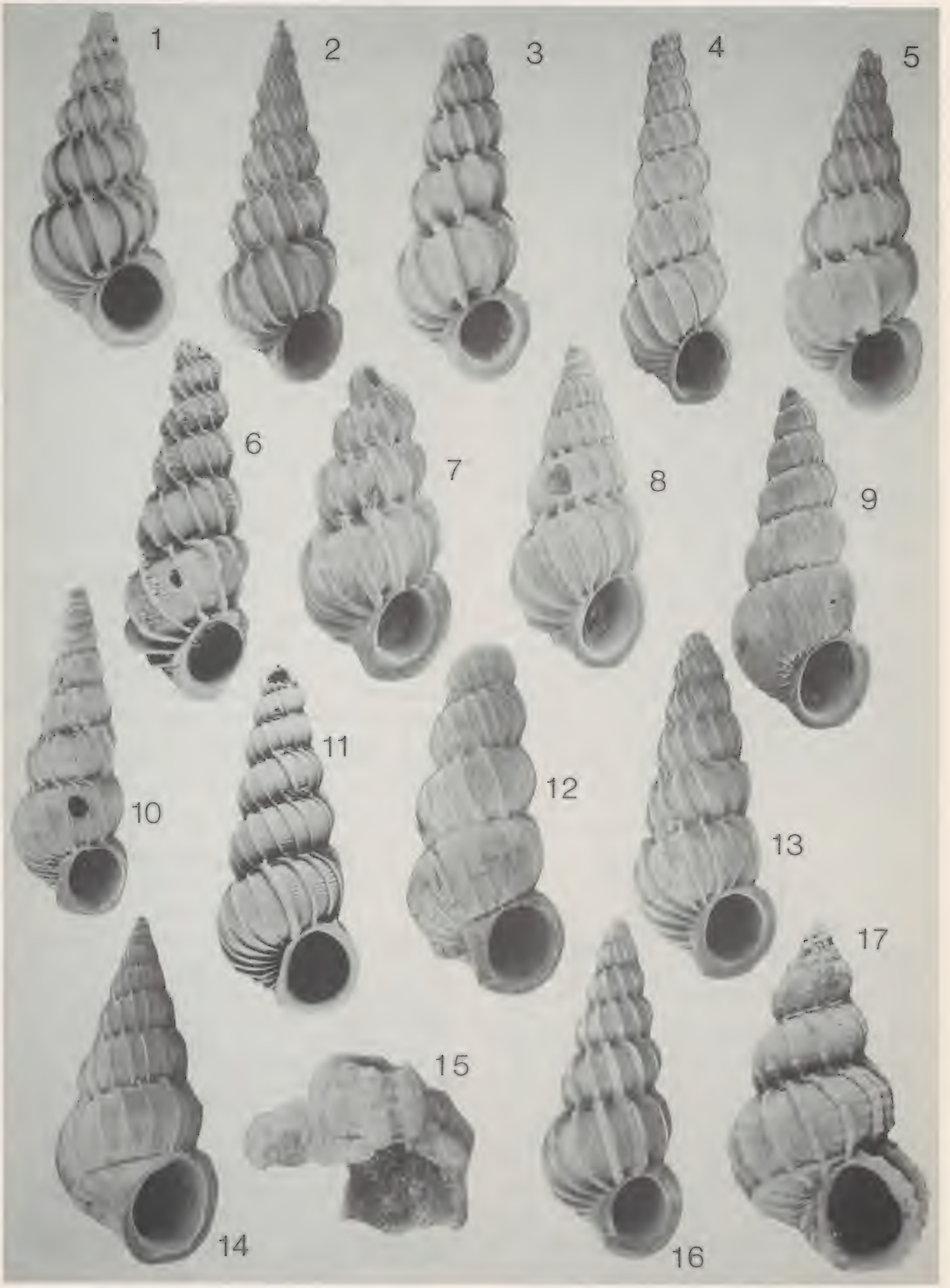

PLATE 3

16. DEPRESSISCALA aff. NITIDELLA (Dall, 1889) 38
MPEF-PI-072 (hypotype); length: 13 mm; width: 5 mm (nuclear whorls broken).
Locality: Baliz Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
17. OPALIOPSIS LINARESI, n. sp. 38
MPEF-PI-130 (holotype); height: 14 mm; width: 8 mm.
Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

EPITONIUM (EPITONIUM) HUMPHREYSII (Kiener, 1838)
Plate 3, figure 3

Description: Shell rather strong in structure, imperforate; five and one-half whorls. Spire high, forming an angle of 26 degrees. Aperture subcircular, outer lip expanded and thick. Parietal lip thin, appressed to the body whorl. Columella short and arched. Suture deep. Sculpture consisting of eight costae on the last whorl, slightly reflected backwards and angled at whorl shoulder. Costae finer on early whorls, becoming more rounded and thicker. No microscopic sculpture on the later whorls.

Hypotype: MPEF-PI-059; length: 14.5 mm; width: 5.5 mm (broken).

Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Discussion: There is not much variation between these specimens and those living in the western Atlantic Ocean, particularly with the examples from South Carolina. *Epitonium humphreysii* (Kiener, 1838) is reported for the first time from the Entrerriense Formation of South America.

EPITONIUM (EPITONIUM) HUMPHREYSII (Kiener, 1838)
Lámina 3, figura 3

Descripción: Concha más bien fuerte en estructura, imperforada; cinco y media vueltas. Espira alta formando un ángulo de 26 grados. Abertura subcircular, labio externo expandido y grueso. Labio parietal delgado, adosado al habitáculo. Columela corta y arqueada. Suturas profundas. La escultura consiste en ocho costillas axiales en la última vuelta, debilmente reflejadas hacia atrás y anguladas a nivel del hombro. Las costillas son más finas en las primeras vueltas, haciendose más redondeadas y gruesas en las últimas. No se observa estructura microscópica.

Hipotipo: MPEF-PI-059; altura: 14,5 mm; ancho: 5,5 mm.

Localidad: Puerto Pirámide. Península Valdés, Provincia del Chubut, Argentina.

Discusión: No existen grandes variaciones entre los especímenes fósiles y los vivientes en el oeste del Océano Atlántico, particularmente con la que habita Carolina del Sur. *Epitonium humphreysii* (Kiener, 1838) se menciona por primera vez para la Formación Entrerriense de Sudamérica.

EPITONIUM (EPITONIUM) LEPTOSOMUM, n. sp.
Plate 3, figure 4

Description: Shell rather light in structure, imperforate. Spire extended, forming an angle of 20 degrees; nine and one-half convex whorls, attached by costae only. Aperture oval, outer lip thick and not very reflected. Parietal lip narrow and appressed to body whorl by a shield. Columella short and arched. Suture deep. Sculpture consisting of 11 thin, rounded costae on last whorl, strongly angled on anterior part. No basal ridge.

Holotype: MPEF-PI-061; length: 12.5 mm; width: 4 mm (the early whorls broken).

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: So named for its thin shape.

Discussion: Epitonium leptosomum, n. sp., differs from *Epitonium tollini* Bartsch,

EPITONIUM (EPITONIUM) LEPTOSOMUM, n. sp.
Lámina 3, figura 4

Descripción: Concha más bien débil en estructura, imperforada. Espira elevada, formando un ángulo de 20 grados; nueve y media vueltas convexas, unidas solo por las costillas. Abertura oval, labio externo grueso pero no muy reflejado. Labio parietal angosto y adherido al habitáculo Suturas profundas. Escultura consistente en 11 costillas finas y redondeadas en la última vuelta, fuertemente anguladas en su parte anterior. Sin costilla basal.

Holotipo: MPEF-PI-061; altura 12,5 mm; ancho: 4 mm (primeras vueltas rotas).

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por su escuálida estructura.

Discusión: Epitonium leptosomum, n. sp., difiere de *Epitonium tollini* Bartsch,

1938, which has an umbilical shield and a strong angulation of the anterior part of the costae on the body whorl. It differs from *Epitonium georgettina* (Kiener, 1839) in being narrower, with only 11 costae, which are not reflected, and a strong angulation of the anterior part of the costae on the body whorl.

EPITONIUM (EPITONIUM)
UNIFASCIATUM (Sowerby, 1844)
Plate 3, figure 5

Description: Shell rather light in structure, imperforate. Spire high, forming an angle of 20 degrees; six and one-half convex whorls atttached only by the costae. Aperture subcircular, outer lip slightly reflected and moderately thickened. Parietal lip well defined. Suture deep. Sculpture consisting of nine blade-like costae, more rounded on body whorl. Costae on each whorl aligned with those of the preceding whorl. No spiral ornamentation or basal ridge.

Hypotype: MPEF-PI-062; length: 13 mm; width: 5 mm (nuclear whorls broken).

Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Discussion: We can detect no differences between the fossil specimens and those living in the western Atlantic Ocean. This species was reported for the Entrerriense Formation of Colonia, Uruguay (Camacho Formation) by Figueiras and Broggi (1971-73), and for the first time from Chubut Province in this work.

EPITONIUM (EPITONIUM)
CINGOLANII, n. sp.
Plate 3, figure 6

Description: Shell of six and one-half whorls, rather light in structure, imperforate. Spire high and whorls attached only by the costae. Aperture suboval, outer lip expanded, faintly reflected, inner lip narrow and attached to body whorl by costae fused to it. Columella not definable. Suture deep. Sculpture consisting of eight blade-like, reflected costae on body whorl. Costae with two angles, one at whorl shoulder, the other at anterior part of costae; tips of these angles concavely sloped backwards. Neither microscopic sculpture nor basal ridge.

Holotype: MPEF-PI-063; length: 11.5 mm; width: 4 mm (nuclear whorls broken).

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

1938, por tener un escudo umbilical y fuerte angulación anterior de las costillas del habitáculo. Difiere de *Epitonium georgettina* (Kiener, 1839) por ser mucho más angosto, tener 11 costillas, no reflejadas y fuerte angulación anterior en las costillas del habitáculo.

EPITONIUM (EPITONIUM)
UNIFASCIATUM (Sowerby, 1844)
Lámina 3, figura 5

Descripción: Concha más bien liviana en estructura, imperforada. Espira alta, formando un ángulo de 20 grados; seis y media vueltas convexas unidas solo por las costillas. Abertura subcircular, labio externo levemente reflejado y moderadamente engrosado. Labio parietal bien definido. Suturas profundas. La escultura consiste en nueve costillas laminares, más redondeadas en el habitáculo. Las costillas de cada vuelta se alinean con las de la vuelta precedente. Sin ornamentación concéntrica ni costilla basal.

Hipotipo: MPEF-PI-062; altura: 13 mm; ancho: 5 mm (vueltas nucleares rotas).

Localidad: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Discusión: No hemos observado diferencias manifiestas entre los especímenes fósiles y los vivientes en el oeste del Océano Atlántico. Esta especie es mencionada para la Formación Entrerriense de Colonia, Uruguay (Formación Camacho) por Figueiras y Broggi (1971-73) y por primera vez para la Provincia del Chubut en este trabajo.

EPITONIUM (EPITONIUM)
CINGOLANII, n. sp.
Lámina 3, figura 6

Descripción: Concha con seis y media vueltas, más bien débil en estructura, imperforada. Espira alta y vueltas unidas solo por las costillas. Abertura suboval, labio externo expandido, apenas reflejado; labio parietal angosto y unido al habitáculo por las costillas soldadas a el. Columela no definida. Suturas profundas. La escultura consiste en ocho costillas laminares y reflejadas en el habitáculo. Las costillas tienen doble angulación, una a la altura del hombro y la otra en la parte anterior; las angulaciones superiores son cóncavas y con declive hacia atrás. Sin estructura microscópica ni costilla basal.

Holotipo: MPEF-PI-063; altura: 11,5 mm; ancho: 4 mm (vueltas nucleares rotas).

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicated to the geologist Dr. Carlos A. Cingolani.

Discussion: Epitonium cingolanii, n. sp., differs from *Epitonium foliaceicostatum* (d'Orbigny, 1842) in being smaller, lighter in structure and with a narrow spire. The length/width index of the latter species is 2.5; for the new species it is 3.3. It has no intercostal spiral lines. *Epitonium krebsii* (Mörch, 1874) differs in being umbilicate, stronger in structure, and has the angle of the whorl shoulders less developed; the length/width index of the latter species is 1.7.

Derivatio nominis: Dedicado al geólogo Dr. Carlos A. Cingolani.

Discusión: Epitonium cingolanii, n. sp., difiere de *Epitonium foliaceicostatum* (d'Orbigny, 1842) por ser más pequeño, más débil en estructura y con espira más angosta. El índice largo/ancho de esta última especie es 2.5; para la nueva especie es de 3.3, no presentando estriás intercostales concéntricas. Difiere de *Epitonium krebsii* (Mörch, 1874) por ser ésta umbilicada, más fuerte en estructura y tener las angulaciónes a nivel del hombro poco desarrolladas; el índice largo/ancho de esta ultima especie es de 1.7.

EPITONIUM (EPITONIUM) VENOSUM (Sowerby, 1844)
Plate 3, figure 7

Description: Shell rather strong in structure, imperforate; three and one-half moderately convex whorls, attached by costae only. Spire forming an angle of 20 degrees. Aperture subcircular, outer lip expanded and reflected. Parietal lip narrow and attached to body whorl by costae only. Columella not readily definable; aperture holostomatous. Suture deep. Sculpture consisting of nine blade-like costae, curved backwards, with a slight angulation of costae at whorl shoulder; costae of each whorl aligned with those of preceding whorl. Microscopic sculpture consisting of fine spiral threads, only under strong magnification.

Hypotype: MPEF-PI-064; length: 7.5 mm; width: 3.8 mm (early whorls broken).

Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Discussion: There are no important features differentiating the fossil specimens from the living specimens. One of our specimens resembles the holotype of *Scalaria erectispina* (Mörch, 1874) [which is considered synonymous with *Epitonium venosum*] from St. Thomas, Virgin Islands (Clench and Turner, 1951, pl. 115); it has nine costae on the body whorl. Other specimens with a higher spire resemble the specimens from Puerto Cabello (Venezuela), with 11 costae on the body whorl. This species is reported for the first time from the Entrerriense Formation of South America.

EPITONIUM (EPITONIUM) VENOSUM (Sowerby, 1844)
Lámina 3, figura 7

Descripción: Concha más bien fuerte en estructura, imperforada; tres y media vueltas moderadamente convexas y unidas solo por las costillas. Espira formando un ángulo de 20 grados. Abertura subcircular, labio externo expandido y reflejado. Labio parietal angosto y unido al habitáculo solo por las costillas. Columela debilmente notoria; apertura holostomada. Suturas profundas. La escultura consiste en nueve costillas laminares, curvadas hacia atrás, con débil angulación a nivel del hombro; las costillas de cada vuelta se alinean con las de la vuelta precedente. La estructura microscópica consiste en finas estrías espirales, visibles solo bajo fuerte aumento.

Hipotipo: MPEF-PI-064; altura: 7,5 mm; ancho: 3,8 mm (vueltas nepionicas rotas).

Localidad: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Discusión: No se observan importantes caracteres diferenciales entre los especímenes fósiles y los vivientes. Uno de nuestros especímenes es muy similar al holotipo de *Scalaria erectispina* (Mörch, 1874) [considerado sinonimo de *Epitonium venosum]* de Sto. Thomas, Islas Vírgenes (Clench y Turner, 1951, pl. 115), que tiene nueve costillas en el habitáculo. Otros, con espira algo más alta, se asemejan a los especímenes de Puerto Cabello (Venezuela), con 11 costillas en el habitáculo. Esta especie fósil es mencionada por primera vez para la Formación Entrerriense de Sudamérica.

EPITONIUM (EPITONIUM) GEORGETTINA (Kiener, 1839)
Plate 3, figure 8

EPITONIUM (EPITONIUM) GEORGETTINA (Kiener, 1839)
Lámina 3, figura 8

Description: Shell rather light in structure, imperforate; five and one-half strongly convex and slightly separated whorls, attached by costae only. Spire extended, forming an angle of 20 degrees. Aperture subcircular and holostomatous. Outer lip slightly reflected, parietal lip usually in form of a shield which covers the costae. Columella poorly defined. Suture deep. Sculpture consisting of 10 to 12 rather low, narrow and slightly reflected costae on body whorl. No spiral sculpture or basal ridge.

Hypotype: MPEF-PI-065; length: 9 mm; width: 4 mm.

Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Discussion: The fossil specimens resemble those living in Golfo Nuevo, Golfo San José, and Punta Norte (Chubut Province) with a low spire, from 13 to 15 mm in height. The living specimens from Golfo San Matías (Rio Negro Province) reach 15-30 mm in height. This species is reported for the first time from the Entrerriense Formation of Chubut Province.

Descripción: Concha más bien débil en estructura, imperforada; cinco y media vueltas fuertemente convexas y ligeramente separadas, unidas solo por las costillas. Espira elevada, formando un ángulo de 20 grados. Abertura subcircular y holostomada. Labio externo reflejado levemente, labio parietal usualmente con un escudo que cubre las costillas. Columela debilmente definida; suturas profundas. La escultura consiste en 10 a 12 costillas, más bien bajas, angostas y debilmente reflejadas en el habitáculo. Sin escultura espiral ni costilla basal.

Hipotipo: MPEF-PI-065; altura: 9 mm; ancho: 4 mm.

Localidad: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Discusión: Los especímenes fósiles se asemejan a los vivientes en Golfo Nuevo, Golfo San José y Punta Norte (Provincia del Chubut) con espira baja y una altura que oscilla entre 13 y 15 mm. Los del Golfo San Matías (Provincia del Rio Negro) miden entre 15 mm y 30 mm de altura. Esta especie es mencionada por primera vez para la Formación Entrerriense de la Provincia del Chubut.

Subgenus ASPERISCALA de Boury, 1909
EPITONIUM (ASPERISCALA) MULTISTRIATUM (Say 1826)
Plate 3, figure 9

Description: Shell attenuate, imperforate and rather light in structure, five and one-half strongly convex whorls. Aperture subcircular, with a narrow expanded lip. Parietal lip moderately developed and appressed tightly to body whorl. Columella poorly defined. Suture deeply impressed. Axial sculpture consisting of 19 fine, low costae, not forming angles at whorl shoulder. Spiral sculpture consisting of numerous fine incised lines, not passing over costae. No basal ridge.

Hypotype: MPEF-PI-069; length: 11.5 mm; width: 5 mm (nuclear whorls broken).

Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Discussion: We can detect no differences in the features exhibited by this fossil and the specimens living in the western Atlantic Ocean. This species is reported for the first time from the Entrerriense Formation of South America.

EPITONIUM (ASPERISCALA) TONNII, n. sp.
Plate 3, figure 10

Subgénero ASPERISCALA de Boury, 1909
EPITONIUM (ASPERISCALA) MULTISTRIATUM (Say, 1826)
Lámina 3, figura 9

Descripción: Concha delgada, imperforada y más bien débil en estructura; cinco y media vueltas fuertemente convexas. Abertura subcircular, con una angosta expansión labial. Labio parietal moderadamente desarrollado y estrechamente adosado al habitáculo. Columela debilmente definida. Suturas profundamente impresas. Escultura axial consistente en 19 finas y bajas costillas, sin angulación en el hombro. Escultura concéntrica consistente en numerosas y finas estrías que no pasan por encima de las costillas. Sin costilla basal.

Hipotipo: MPEF-PI-069; altura: 11,5 mm; ancho: 5 mm (vueltas nepiónicas rotas).

Localidad: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Discusión: No hemos observado diferencias estructurales entre el espécimen fósil y los vivientes en el oeste del Océano Atlántico. Esta especie es mencionada por primera vez para la Formación Entrerriense de Sudamérica.

EPITONIUM (ASPERISCALA) TONNII, n. sp.
Lámina 3, figura 10

Description: Shell rather light in structure; seven and one-half strongly convex whorls, attached by costae only. Aperture ovate with a narrow and slightly reflected outer lip. Parietal lip moderately developed and appressed to body whorl by a small shield. Columella poorly defined. Suture deep. Axial sculpture consisting of 19 low and narrow costae with a fine hook on whorl shoulder. Spiral sculpture consisting of numerous strong striae, with other finer, low threads intercalated between major ones.

Holotype: MPEF-PI-066; length: 13 mm; width: 4.5 mm (nuclear whorls broken).

Type locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the paleontologist Dr. Eduardo Tonni of the Vertebrate Paleontology Division of La Plata Museum.

Discussion: Epitonium (Asperiscala) tonnii, n. sp., differs from *Epitonium (Asperiscala) babylonium* (Dall, 1889), which has a greater number of costae (24 on the body whorl), is much higher spired, and lacks the intermediate spiral striae. *Epitonium (Asperiscala) novangliae* (Couthouy, 1838) differs in being umbilicate, lacking a parietal shield and the intermediate spiral striae; also having a lesser number of costae (14 on body whorl).

Descripción: Concha más bien delgada en estructura; siete y media vueltas fuertemente convexas, unidas solamente por las costillas. Abertura oval con un estrecho y algo reflejado labio externo. Labio parietal moderadamente desarrollado y adosado al habitáculo por un pequeño escudo. Columela debilmente definida. Suturas profundas. Escultura axial consistente en 19 costillas bajas y angostas, con un fino gancho en el hombro. Escultura espiral constituída por numerosas y fuertes estrías, con otras mas finas y bajas intercaladas entre las mayores.

Holotipo: MPEF-PI-066; altura: 13 mm; ancho: 4,5 mm (vueltas nepiónicas rotas).

Localidad tipo: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al paleontólogo Dr. Eduardo Tonni, de la División Paleontología de Vertebrados del Museo de la Plata.

EPITONIUM (ASPERISCALA) aff.
NOVANGLIAE (Couthouy, 1838)
Plate 3, figure 11

Description: Shell rather light in structure, umbilicate; nine and one-half strongly convex whorls, with early whorls attached, later ones attached by costae only. Aperture ovate with a narrowly expanded lip. Parietal lip moderately developed, and attached to body whorl. Columella weakly defined. Suture deeply impressed. Umbilicus narrow and partially hidden by parietal lip. Axial sculpture consisting of 14 blade-like costae on body whorl; on whorl shoulder a small angulation developed on each costa. Spiral sculpture consisting of numerous fine, low striae.

Hypotype: MPEF-PI-067; length: 15.5 mm; width: 5 mm (nuclear whorls broken).

Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Discussion: This fossil specimen differs from *Epitonium (Asperiscala) novangliae* (Couthouy, 1838) in that it is umbilicate; therefore, we only tentatively assign it to the indicated species. It is separated from

EPITONIUM (ASPERISCALA) aff.
NOVANGLIAE (Couthouy, 1838)
Lámina 3, figura 11

Descripción: Concha más bien débil en estructura, umbilicada; nueve y media vueltas fuertemente convexas, las primeras unidas entre sí, las últimas solo unidas por las costillas. Abertura oval con un angosto labio externo. Labio parietal moderadamente desarrollado y unido al habitáculo. Columela debilmente definida. Suturas profundamente impresas. Ombligo angosto y parcialmente oculto por el labio parietal. Escultura axial consistente en 14 costillas laminares en el habitáculo; a la altura del hombro se observa una pequeña angulación en cada costilla. La escultura espiral consiste en numerosas estrías concéntricas muy finas y bajas.

Hipotipo: MPEF-PI-067; altura: 15,5 mm, ancho: 5 mm (vueltas nepiónicas rotas).

Localidad: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Discusión: Este espécimen fósil difiere de *Epitonium (Asperiscala) novangliae* (Couthouy, 1838) por ser umbilicada; por ello solo lo asignamos tentativamente a la especie indicada. La separa de *Epitonium*

Epitonium (Asperiscala) denticulatum (Sowerby, 1844) by the lack of a parietal shield, the higher and narrower spire and the greater number of costae. This species was reported from the Cuenca de Pelotas (southern Brazil) by Closs (1970) and is described for the first time from the Entrerriense Formation of Argentina.

EPITONIUM (ASPERISCALA)
CHUBUTINUM (Ihering, 1907)
Plate 3, figure 12

Description: Shell rather light in structure. Spire extended, forming an angle of 20 degrees; four and one-half very convex whorls. Aperture oval and holostomatous, with a narrow and expanded lip. Parietal lip with a large shield over the costae, covering umbilical area. Suture deep. Axial sculpture of 16 costae on body whorl, low and blade-like, with two or three varices on each whorl. Costae of one whorl aligned with those of whorl above, varices with hook on whorl shoulder. Spiral scupture consisting of numerous intercostal axial striae.

Hypotype: MPEF-PI-068; length: 12 mm; width: 5 mm (only 2 1/2 whorls).

Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Discussion: This specimen resembles the holotype from Puerto Pirámide (Chubut Province) described by Ihering (1907). Our specimen differs in that it has a larger shield covering the umbilical area, and low blade-like costae.

EPITONIUM (ASPERISCALA)
QUIROGAI, n. sp.
Plate 3, figure 13

Description: Shell small, conical, not umbilicate; six and one-half whorls, lacking the nepionic whorls. Whorls slightly globose and somewhat low. Last whorl with 11 blade-like axial costae, low and somewhat recurved, including two heavy varices. Costae angulated at the shoulder, forming a strong spine, directed toward the suture in a concave form. Spiral ornamentation consisting of 14 fine flat equal cords, which do not pass over the costae. Aperture oval, with heavy peristome, the same thickness as the varices and with spines similar to those of the costae. Suture not very deep. In the umbilical zone the two primary ribs are fused to the parietal lip; the three following are introduced below the same; but the three remaining form an angle of 90 degreess, appressed to the peristome.

(Asperiscala) denticulatum (Sowerby, 1844) la ausencia de escudo parietal, espira más alta y más angosta y un mayor número de costillas. Esta especie ha sido mencionada para la Cuenca de Pelotas (Sur de Brasil) por Closs (1970) y es descripta por primera vez para la Formación Entrerriense de Argentina.

EPITONIUM (ASPERISCALA)
CHUBUTINUM (Ihering, 1907)
Lámina 3, figura 12

Descripción: Concha débil en estructura. Espira elevada, formando un ángulo de 20 grados; cuatro y media vueltas muy convexas. Abertura oval y holostomada, labio externo fino y expandido. Labio parietal con un fuerte escudo sobre las costillas, cubriendo el área umbilical. Suturas profundas. Escultura axial con 16 costillas en el habitáculo, bajas y laminares, con dos o tres várices en cada vuelta. Las costillas de una vuelta están en linea con las de la vuelta precedente; las várices poseen un gancho a nivel del hombro. La escultura espiral consiste en numerosas estrías intercostales.

Hipotipo: MPEF-PI-068; altura: 12 mm; ancho: 5 mm (solo dos y media vueltas).

Localidad: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Discusión: Este espécimen se asemeja al holotipo de Puerto Pirámide (Provincia del Chubut) descrito por Ihering (1907). Nuestro espécimen difiere por poseer un escudo en el área umbilical y costillas más finas y más bajas.

EPITONIUM (ASPERISCALA)
QUIROGAI, n. sp.
Lámina 3, figura 13

Descripción: Concha pequeña, cónica, no umbilicada; seis y medio anfractos, faltando las vueltas nepiónicas. Anfractos poco globosos y algo bajos. Ultimo anfracto con 11 costillas axiales, laminares, bajas y algo recurvadas que incluyen dos gruesas várices. A nivel del hombro las costillas se angulan, formando una fuerte espina, dirigiendose hacia la sutura en forma cóncava. Ornamentación concéntrica constituída por finos, planos e iguales cordones en número de 14, que no pasan sobre las costillas. Abertura oval, con peristoma grueso, del mismo espesor que las várices y con espina similar a las de las costillas. Sutura poco profunda. En la zona umbilical, las dos primeras costillas se sueldan al labio parietal; las tres siguientes se introducen por debajo del mismo; mientras que las tres restantes describen un ángulo de 90 grados, adosandose al peristoma.

Holotype: MPEF-PI-006; length: 11 mm; width: 4.5 mm; height of last whorl: 3 mm. Aperture: length 2 mm, width 1.4 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late neuropaleontologist Dr. Juan Carlos Quiroga.

Discussion: Epitonium (Asperiscala) quirogai, n. sp., differs from *Epitonium chubutina* (Ihering, 1907), described from Puerto Pirámide, by being much shorter, having a total length of 11 mm, but in the latter the last four whorls measure 10 mm in length. The last whorl of *Epitonium chubutina* has a height of 3.5 mm and a diameter of 5 mm; but *Epitonium (Asperiscala) quirogai* has a height of 3 mm and a diameter of 4.5 mm; the suture of the latter is not as deep as the former. In *Epitonium chubutina* there are 13 costae on the last whorl and *Epitonium (Asperiscala) quirogai* has only 11. The latter has denticles on all of the costae but in *Epitonium chubutina* these are present only on the varices. The spiral cords of this latter species are heavy and elevated almost up to the costal height, but in the new species they are fine and flat. *Epitonium borcherti* (Ihering, 1907), has more rounded whorls, especially the last; costae with posterior teeth and lacking the spiral ornamentation. The number of costae is ten. With respect to other examples of *Epitonium* sp. obtained by F. Ameghino in an excavation in Buenos Aires, the number of costae is 15 per whorl and it does not have denticulated posterior costae. *Epitonium (Asperiscala) quirogai* differs from *Epitonium (Asperiscala) novangliae* (Couthouy, 1838) by having more convex whorls, a cancellate ornamentation, and it is umbilicate. The same differences are observed with *Epitonium (Asperiscala) denticulatum* (Sowerby, 1844). But *Epitonium (Asperiscala) pourtalesii* (Verrill and Bush, 1880) differs by being umbilicate, by its cancellate structure and by the parietal shield placed near the costae.

Subgenus GYROSCALA de Boury, 1887

EPITONIUM (GYROSCALA) CIONEI, n. sp.

Plate 3, figure 14

Holotipo: MPEF-PI-006; largo: 11 mm; ancho: 4,5 mm; altura del último anfracto: 3 mm. Abertura: largo 2 mm, ancho 1,4 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al difunto neuropaleontólogo Dr. Juan Carlos Quiroga.

Discusión: Epitonium (Asperiscala) quirogai, n. sp., difiere de *Epitonium chubutina* (Ihering, 1907) proveniente de Puerto Pirámide, por ser mucho más corta, dado que su largo total es de 11 mm, mientras que en la segunda, las últimas cuatro vueltas miden 10 mm de largo. La última vuelta de *Epitonium chubutina* tiene un alto de 3,5 mm y un diámetro de 5 mm; mientras que en *Epitonium (Asperiscala) quirogai* tiene un alto de 3 mm y un diámetro de 4,5 mm; la sutura en esta última no es tan profunda como en la antedicha. En *Epitonium chubutina* se cuentan 13 costillas axiales en el último anfracto y *Epitonium (Asperiscala) quirogai* tiene solo 11. Esta última tiene dentículos en todas las costillas mientras que en *Epitonium chubutina* se hallan presentes solo en las várices. Los cordones concéntricos de esta última especie son gruesos y elevados casi hasta la altura costal, mientras que en la nueva especie son finos y planos. Respecto a *Epitonium borcherti* (Ihering, 1907) posee vueltas más redondeadas, especialmente la última; costillas sin dientes posteriores y ausencia de ornamentación concéntrica. El número de costillas es de diez. Con respecto a otro ejemplar de *Epitonium* sp. obtenido por F. Ameghino en una excavación en Buenos Aires, el número de costillas es de 15 por vuelta y no posee dentículos posteriores costales. *Epitonium (Asperiscala) quirogai* difiere de *Epitonium (Asperiscala) novangliae* (Couthouy, 1838) por tener ésta anfractos más convexos, una ornamentación cancellada y ser umbilicada. Las mismas diferencias se observan para *Epitonium (Asperiscala) denticulatum* (Sowerby, 1844). Mientras que *Epitonium (Asperiscala) pourtalesii* (Verrill y Bush, 1880); difiere por ser umbilicado, por su estructura cancellada y por su escudo parietal adosado a las costillas.

Subgénero GYROSCALA de Boury, 1887

EPITONIUM (GYROSCALA) CIONEI, n. sp.

Lámina 3, figura 14

Description: Shell rather light in structure, imperforate; eight and one-half convex whorls. Spire not very extended, forming an angle of 33 degrees. Aperture oval. Outer lip slightly reflected and narrow. Parietal lip narrow and appressed tightly to body whorl. Columella weakly defined, aperture holostomatous. Suture well defined and deep. Sculpture consisting of 15 blade-like axial costae, not aligned with those of preceding whorl. Basal ridge well developed and lacking varices.

Holotype: MPEF-PI-070; length: 10.5 mm; width: 5 mm (nuclear whorls broken).

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the paleontologist Dr. Albert Cione of the Vertebrate Paleontology Division of La Plata Museum.

Discussion: Epitonium (Gyroscala) cionei, n. sp., differs from *Epitonium (Gyroscala) rupicolum* (Kurtz, 1860), which has varices and an outer lip that is thicker and more reflected; the basal ridge is weaker and the inner lip is not defined. The new species differs from *Epitonium (Gyroscala) lamellosum* (Lamarck, 1822), which only has ten costae, all aligned with the preceding whorl, and the spire forms an angle of 40 to 50 degrees.

Genus CYLINDRISCALA de Boury, 1912

CYLINDRISCALA sp.
Plate 3, figure 15

Description: Shell very incomplete. Axial sculpture consisting of strong cords formed by seven or eight finer cords, joined together. Spiral sculpture consisting of four strong cords, thinner than axial costae and not passing over them, except for one appressed to suture. Suture very irregular, according to development and interpolation of the axial cords.

Hypotype: MPEF-PI-071; measurement impractical.

Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Discussion: Only one-half a whorl of this specimen has been preserved, but it is possible to observe the axial sculpture consists of four strong cord-like costae each one formed by seven or eight finer cords. This is the first report of the genus *Cylindriscala* from the Entrerriense Formation of South America.

Genus DEPRESSISCALA de Boury, 1909

Descripción: Concha más bien delgada en estructura, imperforada; ocho y media vueltas convexas. Espira no muy elevada, formando un ángulo de 33 grados. Abertura oval. Labio externo apenas reflejado y angosto. Labio parietal angosto y fuertemente adherido al habitáculo. Columela debilmente definida, abertura holostomada. Suturas bien definidas y profundas. La escultura consiste en 15 costillas laminares axiales, no alineadas con las de la vuelta precedente. Costilla basal bien desarrollada y ausencia de várices.

Holotipo: MPEF-PI-070; altura: 10,5 mm; ancho: 5 mm (vueltas nucleares rotas).

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicada al paleontólogo Dr. Alberto Cione, de la Division Paleontología de Vertebrados del Museo de La Plata.

Discusión: Epitonium (Gyroscala) cionei, n. sp., difiere de *Epitonium (Gyroscala) rupicolum* (Kurtz, 1860) por tener ésta várices, el labio grueso, fuerte y reflejado, las costilla basal es más débil y el labio interno no definido. Difiere de *Epitonium (Gyroscala) lamellosum* (Lamarck, 1822), el cual tiene solo diez costillas, todas alineadas con la de la vuelta precedente y la espira forma un ángulo de 40 a 50 grados.

Género CYLINDRISCALA de Boury, 1912

CYLINDRISCALA sp.
Lámina 3, figura 15

Descripción: Concha muy incompleta. La escultura axial consiste en fuertes cordones formados por siete o ocho cordones más finos, unidos entre si. La escultura espiral constituída por cuatro fuertes cordones, más delgados que los axiales, no pasando por encima de ellos, excepto uno que va adosado a la sutura. La sutura es muy irregular y acorde con el desarrollo e interpolación de los cordones axiales.

Hipotipo: MPEF-PI-071 (medidas impracticables).

Localidad: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Discusión: Se ha conservado solo una vuelta en este especímen pero es posible observar la escultura axial consistente en cuarto fuertes cordones, formados cada uno por siete u ocho cordones más finos. Esta es la primera mención del género *Cylindriscala* para la Formación Entrerriense de Sudamérica.

Género DEPRESSISCALA de Boury, 1909

DEPRESSISCALA aff. NITIDELLA
(Dall, 1889)
Plate 3, figure 16

Description: Shell with strongly globose attached whorls. Spire high, forming an angle of about 28 degrees. Aperture subovate with parietal area nearly straight. Columella weakly defined. Suture marked but not deep. Axial sculpture consisting of nine strongly reflected, blade-like costae, resembling cords. Neither spiral sculpture nor basal ridge. Umbilicus covered by parietal wall, with costae entering in a spiral formation.

Hypotype: MPEF-PI-072; length: 13 mm; width: 5 mm (nuclear whorls broken).

Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Discussion: For the first time the genus *Depressiscala* is reported from the Entrerriense Formation of South America. The fossil specimen differs from the living species *Depressiscala nitidella* (Dall, 1889) in that it has no visible spiral sculpture. The measurements of the fossil specimens are identical to the holotype from Cape Hatteras, North Carolina (USA), station number 2596, in 49 fathoms.

DEPRESSISCALA aff. NITIDIELLA
(Dall, 1889)
Lámina 3, figura 16

Descripción: Concha con anfractos globosos y unidos. Espira alta, formando un ángulo de alrededor de 28 grados. Abertura suboval, con área parietal casi recta. Columela debilmente definida. Suturas marcadas pero no profundas. Escultura axial consistente en nueve costillas laminares, fuertemente reflejadas, asemejandose a cordones. Sin escultura espiral ni costilla basal. Ombligo cubierto por las costillas que se curvan entrando en la zona umbilical en forma espiral.

Hipotipo: MPEF-PI-072; altura: 13 mm; ancho: 5 mm (faltan vueltas nepiónicas).

Localidad: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Discusión: Por primera vez el género *Depressiscala* es mencionado para la Formación Entrerriense de Sudamérica. El especímen fósil difiere de la especie viviente *Depressiscala nitidiella* (Dall, 1889) por no tener escultura espiral visible. Las medidas del espécimen fósil coinciden con las del holotipo de Cabo Hatteras, Carolina del Norte (EE.UU.), estación núm. 2596, a 49 fathoms.

Subfamily NYSTIELLINAE
Genus OPALIOPSIS Thiele, 1928
OPALIOPSIS LINARESI, n. sp.
Plate 3, figure 17

Description: Shell globose, turbinate, thin but strong; six strongly convex and attached whorls. Spire moderately extended. Aperture subcircular and holostomatous. Lip reflected and tuberculated. Parietal area with lip attached to costae. Columella weakly defined. Not umbilicate. Sculpture consisting of 12 strong, tuberculated axial costae on last whorl. Spiral sculpture consisting of five or six low ridges, not crossing costae. Basal ridge well developed with axial costae continuing below it; some costae in a spiral formation covering umbilical area.

Holotype: MPEF-PI-130; height: 14 mm; width: 8 mm.

Type locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the geologist Dr. Enrique Linares.

Discussion: Opaliopsis linaresi, n. sp., differs from *Opaliopsis cania* (Dall, 1927), which has a greater number of whorls and resulting higher spire, heavier spiral cords, lacking the spiral form of the costae at the umbilical. level and a basal ridge

Subfamilia NYSTIELLINAE
Género OPALIOPSIS Thiele, 1928
OPALIOPSIS LINARESI, n. sp.
Lámina 3, figura 17

Descripción: Concha globosa, turbinada, delgada pero fuerte; seis vueltas fuertemente soldadas y muy convexas. Espira moderadamente elevada. Abertura subcircular y holostomada. Labio externo reflejado y tuberculado. Area parietal con el labio unido por las costillas. Columela debilmente definida. Sin ombligo. La escultura consiste en 12 costillas axiales fuertes y tuberculadas en la última vuelta. La escultura espiral consiste en cinco o seis costillas bajas que no pasan sobre las axiales. Costilla basal bien desarrollada, con las costillas axiales continuandose por debajo de ella; algunas costillas en forma espiral cubren el área umbilical.

Holotipo: MPEF-PI-130; altura: 14 mm; ancho: 8 mm.

Localidad tipo: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al geólogo Dr. Enrique Linares.

Discusión: Opaliopsis linaresi, n. sp., difiere de *Opaliopsis cania* (Dall, 1927) por tener ésta mayor número de vueltas y por consiguiente espira más alta, cordones espirales más gruesos, ausencia de forma es-

proportionally less developed. It differs from *Opaliopsis azelotes* (Dall, 1927), which has a higher spire, much more strongly developed spiral sculpture, and a lesser number of spiral cords (four); the areas between the cords are square and rather deep; the last cord forms the basal ridge and there are no costae in a spiral covering the umbilical area. This is the first time that the genus *Opaliopsis* has been reported from the Entrerriense Formation of South America.

Superfamily NATICOIDEA
Family NATICIDAE
Subfamily POLINICINAE
Genus NEVERITA Risso, 1826
Subgenus GLOSSAULAX Pilsbry, 1929
NEVERITA (GLOSSAULAX) GROEBERI,
n. sp.
Plate 4, figure 2

Description: Shell ovoid, depressed; spire inconspicuous, two and one-half nuclear whorls and three postnuclear whorls. Suture shallow; last whorl ovoid and depressed. Axial sculpture consisting of heavy and weak growth lines. Aperture semicircular, outer lip anteriorly convex, forming an acute angle posteriorly, elevated above the level of the callus. Columella convex posteriorly and concave anteriorly. Columellar callus wide, slightly projecting. coming from the columella without pronounced distinction, with a depression to the level of the margin of the body whorl, which divides it into two lobes, one anterior and one posterior. The anterior part of the callus appears more elevated than the posterior.

Holotype: MPEF-PI-143; height: 12 mm; width: 18 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Pablo Groeber.

Discussion: Neverita (Glossaulax) groeberi, n. sp., differs from *Neverita (Glossaulax) bolivarensis tapina* Woodring, 1957, from the Gatun Lake area (Panama Canal), which has a very noticeable furrow bordering the umbilical callus and striated umbilical walls. *Neverita (Glossaulax) recluziana xena* Woodring, 1957, from the Transisthmian Highway (Gatun Formation), differs in having the spire more elevated (almost as high as wide), the posterior lobe of the callus completely covers the umbilicus, the interlobular furrow is very marked and the inner margin is straight and sharp.

piral de las costillas a nivel umbilical y costilla basal proporcionalmente menos desarrollada. Difiere de *Opaliopsis azelotes* (Dall, 1927) por tener ésta espira más alta, escultura espiral mucho más desarrollada, con un número inferior de cordones concéntricos (cuatro); las áreas entre medio de los cordones son cuadradas y bastante profundas; el último cordón forma la costilla basal y no posee costillas en espiral cubriendo el área umbilical. Se menciona por primera vez el género *Opaliopsis* para la Formación Entrerriense de Sudamérica.

Superfamilia NATICOIDEA
Familia NATICIDAE
Subfamilia POLINICINAE
Género NEVERITA Risso, 1826
Subgénero GLOSSAULAX Pilsbry, 1929
NEVERITA (GLOSSAULAX) GROEBERI,
n. sp.
Lámina 4, figura 2

Descripción: Concha ovoide; espira poco notoria, dos y media vueltas nucleares y tres vueltas postnucleares. Suturas poco profundas; último anfracto ovoide y deprimido. Escultura axial constituída por gruesas y finas líneas de crecimiento. Abertura semicircular, labro convexo anteriormente, formando un ángulo agudo posteriormente y elevándose sobre el nivel del callo. Columela convexa atrás y cóncava adelante. Callo columelar ancho, pero poco saliente, que nace de la columela sin distinción notoria, con una depresión a nivel del borde del habitáculo, que lo divide en dos lóbulos, uno anterior y otro posterior. Siendo la parte anterior del callo, más elevada que la posterior.

Holotipo: MPEF-PI-143; altura: 12 mm; ancho: 18 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al extinto geólogo Dr. Pablo Groeber.

Discusión: Neverita (Glossaulax) groeberi, n. sp., difiere de *Neverita (Glossaulax) bolivarensis tapina* Woodring, 1957, procedente del area Gatún Lake (Canal de Panamá) por tener ésta un surco muy notorio bordeando el callo umbilical y las paredes umbilicales estriadas. Difiere de *Neverita (Glossaulax) reclusiana xena* Woodring, 1957, procedente de Transisthmian Highway (Gatun Formation) por tener ésta espira más elevada (casi tan alta como ancha), lóbulo posterior del callo ocluyendo ampliamente el ombligo, surco inter-lobular mucho más marcado y el borde interno recto y filoso.

NEVERITA (GLOSSAULAX) KEIDELI, n. sp.
Plate 4, figure 3

Description: Shell small, oviform, narrow, depressed; spire inconspicuous; one and one-half nepionic whorls and three postnepionic whorls. Suture shallow; last whorl ovoid and depressed. Axial sculpture consisting of heavy and fine growth lines, generally more marked toward the umbilical area. Aperture semicircular, very wide anteriorly, with an acute angle posteriorly; columella convex posteriorly and straight anteriorly. The posterior columellar margin folding back on the body whorl, forming an angulation with the outer lip, but the remainder of the internal margin is separated from the callus by a fine groove. The callus totally covers the umbilicus, but is small, with a transverse groove that divides it into two lobes, a small anterior one and a larger posterior one.

Holotype: MPEF-PI-144; height: 8 mm; width: 11 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicted to the late geologist Dr. Juan Keidel.

Discussion: Neverita (Glossaulax) keideli, n. sp., differs from *Neverita (Glossaulax) bolivarensis tapina* Woodring, 1957, from Palenquillo (Canal Zone), which lacks "a wide furrow" bordering the umbilical callus and lacks a groove separating the umbilical callus from the parietal callus, which appears thin and projecting; moreover, the umbilical callus is much smaller and sunken. It differs also in the same characters from *Neverita bolivarensis* Clark (in Clark and Durham, 1946). *Neverita (Glossaulax) reclusiana xena* Wooding, 1957, has an enormous projecting umbilical callus appressed to the parietal callus, lacking the furrow between them, and also has a much higher shell (almost as high as wide).

Subfamily NATICIDAE
Genus NATICA Scopoli, 1777
Subgenus NATICA s.s.
NATICA (NATICA) PASTOREI, n. sp.
Plate 4, figure 4

Description: Shell elongated, spire not very elevated, body whorl globose. Aperture with the columella slightly concave ending in a strong margin, this forming the anterior labral edge. Callus well developed, closing the posterior apertural angle. Funicule strong and large, almost totally closing the umbilicus. Aperture

NEVERITA (GLOSSAULAX) KEIDELI, n. sp.
Lámina 4, figura 3

Descripción: Concha pequeña, ovoiforme, delgada, deprimida; espira poco notoria; una y media vueltas nepiónicas y tres vueltas postnepiónicas. Suturas poco profundas; último anfracto ovoide y deprimido. Escultura axial constituída por gruesas y finas líneas de crecimiento, por lo general más marcadas al llegar al area umbilical. Abertura semicircular, muy amplia anteriormente, en ángulo agudo posteriormente; columela convexa detrás y recta adelante. El borde columelar posterior se repliega sobre el habitáculo formando una angulación con el labro, mientras que el resto del borde interno se encuentra separado del callo por un fino surco. El callo cubre totalmente el ombligo, pero es pequeño, con un surco transversal al labio interno, que lo divide en dos lóbulos, un anterior pequeño y uno posterior más grande.

Holotipo: MPEF-PI-144; altura: 8 mm; ancho: 11 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al extinto geólogo Dr. Juan Keidel.

Discusión: Neverita (Glossaulax) keideli, n. sp., difiere de *Neverita (Glossaulax) bolivarensis tapina* Woodring, 1957, de Palenquilla (Zona de Canal), por no tener "un amplio surco" bordeando el callo umbilical y poseer un surco que separa el callo umbilical del callo parietal, siendo éste fino y saliente, además el callo umbilical es mucho más pequeño y hundido. Difiere también por estos mismos caracteres de *Neverita bolivarensis* Clark (en Clark and Durham, 1946). Difiere de *Neverita (Glossaulax) reclusiana xena* Woodring, 1957, por tener ésta un enorme y saliente callo umbilical soldado al callo parietal, con ausencia del surco entre ambos y concha mucho mas alta (casi tan alta como ancha).

Subfamilia NATICINAE
Género NATICA Scopoli, 1777
Subgénero NATICA s.s.
NATICA (NATICA) PASTOREI, n. sp.
Lámina 4, figura 4

Descripción: Concha elongada, espira no muy elevada, habitáculo muy globoso. Abertura con columela levemente cóncava que termina en un fuerte reborde, formando éste el borde labral anterior. Callo bien desarrollado que ocluye el ángulo apertural posterior. Funículo fuerte y grande que ocluye casi totalmente el ombligo.

ovoid, wider in the posterior part than in the anterior. Axial sculpture consisting of heavy and fine, irregular growth lines.

Holotype: MPEF-PI-127; height: 5 mm; width: 5 mm. Aperture: length 3.5 mm, width 2 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Franco Pastore.

Discussion: Natica (Natica) pastorei, n. sp., differs from *Natica (Natica?) bolus* Brown and Pilsbry, 1913, which lacks the much more developed umbilical callus and the aperture that is much wider posteriorly. *Natica canrena* (Linne, 1767) differs in having a higher spire, and in lacking the anterior columellar border and the axial sculpture. *Natica isabelleana* (d'Orbigny, 1846) differs in having the funicule much smaller, lacking the anterior columellar border, and the axial sculpture is practically nil.

Abertura ovoide, más ancha en la parte posterior que en la anterior. Escultura axial constituída por líneas de crecimiento gruesas y finas, irregulares.

Holotipo: MPEF-PI-127; altura: 5 mm; ancho: 5 mm. Abertura: largo 3,5 mm, ancho 2 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al extinto geólogo Dr. Franco Pastore.

Discusión: Natica (Natica) pastorei, n. sp., difiere de *Natica (Natica?) bolus* Brown y Pilsbry, 1913, por tener un callo umbilical mucho más desarrollado y abertura más amplia posteriormente. Difiere de *Natica canrena* (Linné, 1767) por tener ésta espira mas alta, ausencia del reborde anterior columelar y escultura axial ausente. Difiere de *Natica isabelleana* (d'Orbigny, 1846) por tener ésta funículo mucho más pequeño, ausencia del reborde anterior columelar y escultura axial practicamente nula.

Natica (Natica) borelloi, n. sp.
Plate 4, figure 5

Description: Shell subglobose, tall with a conspicuous projecting spire, whorls semiconvex; umbilicus open and deep, showing the early whorls. Columella straight; lip thin, but reflected toward the outside, especially at the level of the anterior margin. Median callus extending from the posterior angle up to the umbilical margin; funicule weakly developed, with a depression or groove that runs along the entire inner funicular margin, continuing over the columellar margin and ends, forming part of the fold of the anterior margin. External ornamentation consisting of irregular, heavy and fine growth lines. One of our paratypes contained in its interior an operculum that was obtained during the cleaning of the shell hidden in the sediments. It is a calcareous operculum, with an excentric (anterior) nucleus, with a conspicuous peripheral margin and another perinuclear one; also preserved are color striations, possibly due to its premature inclusion within the shell. This description follows the treatment of a fossil operculum without taxonomic connotations.

Holotype: MPEF-PI-145; height: 19 mm; width: 11.5 mm. Aperture: length 9 mm; width 5 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Angel V. Borello.

Discussion: Natica (Natica) borelloi, n. sp., differs from *Natica marochiensis*

Natica (Natica) borelloi, n. sp.
Lámina 4, figura 5

Descripción: Concha subglobosa, alta con espira notoria y prominente, anfractos semiconvexos; ombligo abierto y profundo, mostrando las primeras vueltas. Columela recta; labio fino, pero reflejado hacia afuera, especialmente a nivel del borde anterior. Callo mediano que va desde el ángulo posterior hasta el borde umbilical; funículo poco desarrollado, con una depresión o surco que recorre todo el borde interior funicular, se continúa sobre el borde columelar y termina formando parte del repliegue del borde anterior. Ornamentación externa constituída por estrías de crecimiento irregulares, gruesas y finas. Uno de nuestros paratipos contenía en su interior un opérculo que se obtuvo al efectuar la limpieza de la concha, dado que se encontraba oculto por sedimentos. Se trata de un opérculo calcáreo, con núcleo excéntrico (anterior) con un notorio reborde periférico y otro perinuclear; conservando aún estrías coloreadas, posiblemente por su inclusión prematura dentro de la concha. Esta descripción obedece al hecho de tratarse de un opérculo fósil, sin connotaciones taxonómicas.

Holotipo: MPEF-PI-145; altura: 19 mm; ancho: 11,5 mm. Abertura: largo 9 mm, ancho 5 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al extinto geólogo Dr. Angel V. Borello.

Discusión: Natica (Natica) borelloi, n. sp., difiere de *Natica marochiensis* (Gme-

(Gmelin, 1791), which has a higher spire, more rounded whorls, a larger funicule, a smaller umbilicus and lacks the labial fold. *Natica limbata* d'Orbigny, 1840, has a higher, more pointed spire, lacks the funicule, has the parietal callus much less developed, the umbilicus smaller, and lacks the labral margin. *Natica livida*

lin, 1791) por tener ésta espira más alta, anfractos más redondeados, funículo más grande, ombligo más pequeño y ausencia del repliegue labial. Difiere de *Natica limbata* d'Orbigny, 1840, por tener ésta espira más alta, más aguda, ausencia de funículo, callo parietal mucho menos desarrollado, ombligo más pequeño y ausencia del re-

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PLATE 4

Figure Page

1. LIOTIA TERUGGII, n. sp. 25
MPEF-PI-164 (holotype); height: 11 mm; width: 11 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

2. NEVERITA (GLOSSAULAX) GROEBERI, n. sp. 39
MPEF-PI-143 (holotype); height: 12 mm; width: 18 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

3. NEVERITA (GLOSSAULAX) KEIDELI, n. sp. 40
MPEF-PI-144 (holotype); height: 8 mm; width: 11 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

4. NATICA (NATICA) PASTOREI, n. sp. 40
MPEF-PI-127 (holotype); height: 5 mm; width: 5 mm. Aperture: length 3.5 mm, width 2 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

5. NATICA (NATICA) BORELLOI, n. sp. 41
MPEF-PI-145 (holotype); height: 19 mm; width: 11.5 mm. Aperture: length 9 mm; width 5 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

6. BUCCINANOPS aff. SQUALIDUM (King, 1831) 44
MPEF-PI-010 (hypotype); length 23 mm. Body whorl: length 21 mm, width 14.5 mm. Aperture: length 16 mm; width 6 mm.
Locality: Playa Fracasso, Valdés Peninsula, Chubut Province, Argentina.

7. BUCCINULUM (GLYPTEUTHRIA) aff. AGNESIA (Strebel, 1905) 44
MPEF-PI-135 (hypotype); length: 14 mm; width: 12 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

8. POLYSTIRA sp. 45
MPEF-PI-133 (hypotype); approximate length: 15 mm; width: 8 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

9. BELLASPIRA sp. 45
MPEF-PI-134 (hypotype); length: 11 mm; width: 10.2 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

10. DRILLIA BRACACCINII, n. sp. 46
MPEF-PI-132 (holotype); length: 3 mm; width: 1.2 mm (broken).
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

11. DRILLIA sp. 47
MPEF-PI-131 (hypotype); length: 6 mm; width: 2 mm (broken).
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

12. ISELICA DESSANTII, n. sp. 47
MPEF-PI-165 (holotype); length: 7 mm; width: 5 mm. Aperture: length 3 mm; width 2 mm.
Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

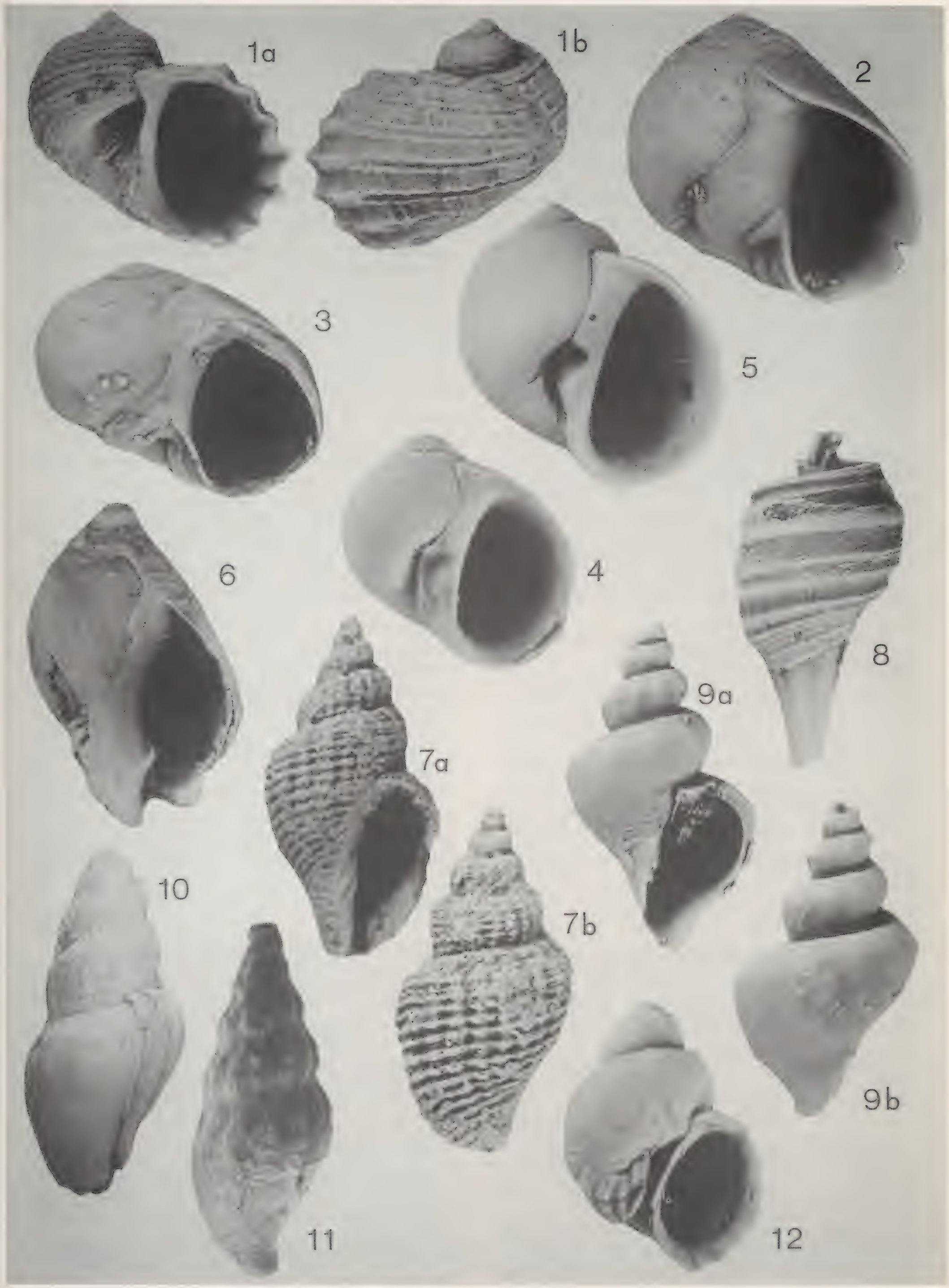

PLATE 4

Pfeiffer, 1840, has more convex whorls, a more developed funicule, which almost totally covers the umbilicus, and lacks the labral margin. This new species is comparable only to living specimens, given that until now there are no known examples of *Natica* in the Tertiary of Patagonia. *Natica entrerriana* Borchert, 1901, was changed by Ihering (1907) to *Polinices entrerriana.*

borde labral. Difiere de *Natica livida* Pfeiffer, 1840, por tener esta anfractos más convexos, funículo más desarrollado, que obtura casi todo el ombligo y ausencia del reborde labral. Esta nueva especie es solo comparable con especímenes vivientes, dado que no se conocen hasta el momento ejemplares de *Natica* para el Terciario de Patagonia. *Natica entrerriana* Borchert, 1901, fue reubicada por Ihering (1907) como *Polinices entrerriana.*

Family NASSARIIDAE
Subfamily DORSANIINAE
Genus BUCCINANOPS d'Orbigny, 1841
BUCCINANOPS aff. SQUALIDUM
(King, 1831)
Plate 4, figure 6

Description: Shell buccinoid, heavy; spire short; last whorl almost five times larger than the spire. Rounded whorls. Aperture elongated with a thin, convex lip, without depression. Columella concave; siphonal canal short, with strong columellar fold and a deep notch.

Hypotype: MPEF-PI-010; length: 23 mm. Body whorl: length 21 mm, width 14.5 mm. Aperture: length 16 mm; width 6 mm.

Locality: Playa Fracasso, Valdés Peninsula, Chubut Province, Argentina.

Discussion: The fossil specimen agrees in its characters with the living species *Buccinanops squalidum* (King, 1831), in spite of the state of the preservation of the shell, which does not permit observation of the presence of spiral striations near the suture. This species is reported for the first time from the Entrerriense Formation of South America.

Familia NASSARIIDAE
Subfamilia DORSANIINAE
Género BUCCINANOPS d'Orbigny, 1841
BUCCINANOPS aff. SQUALIDUM
(King, 1831)
Lámina 4, figura 6

Descripción: Concha bucinoide, gruesa; espira corta; último anfracto casi cinco veces mas largo que la espira. Anfractos redondeados. Abertura alargada con labro convexo, fino y sin depresión. Columela cóncava; canal sifonal corto, con fuerte repliegue columelar y profunda escotadura.

Hipotipo: MPEF-PI-010; largo: 23 mm. Cuerpo del anfracto: largo 21 mm, ancho 14,5 mm. Abertura: largo 16 mm, ancho 6 mm.

Localidad: Playa Fracasso, Península Valdés, Provincia del Chubut, Argentina.

Discusión: El especímen coincide en sus caracteres con la especie viviente *Buccinanops squalidum* (King, 1831), a pesar de que el estado de la concha no permite observar la presencia de estriaciones espirales vecinas a la sutura. Se describe por primera vez la presencia de ésta especie para la Formación Entrerriense de Sudamérica.

Family BUCCINIDAE
Subfamily BUCCININAE
Genus BUCCINULUM Deshayes, 1830
Subgenus GLYPTEUTHRIA
Strebel, 1905
BUCCINULUM (GLYPTEUTHRIA) aff.
AGNESIA (Strebel, 1905)
Plate 4, figure 7

Description: Shell fusiform; spire high, two and one-half nepionic whorls and four and one-half postnepionic whorls, the last occupying more than half of the total length. Whorls convex, suture marked. Sculpture cancellate, with 16 axial and 12 spiral cords on the last whorl. Base of the latter rather excavated; aperture oval; siphonal process short and curved; columella scarcely visible. Outer lip with denticula-

Familia BUCCINIDAE
Subfamilia BUCCININAE
Género BUCCINULUM Deshayes, 1830
Subgénero GLYPTEUTHRIA
Strebel, 1905
BUCCINULUM (GLYPTEUTHRIA) aff.
AGNESIA (Strebel, 1905)
Lámina 4, figura 7

Descripción: Concha fusiforme; espira alta, dos y media vueltas nepiónicas y cuatro y medio anfractos, el último ocupando más de la mitad del largo total. Anfractos convexos y sutura marcada. Escultura cancellada, con 16 cordones axiales y 12 concéntricos en el último anfracto. Base del último bastante excavada; abertura oval; proceso sifonal corto y curvo; columela no bien visible. Labro con denticulaciones que cor-

tions that correspond to the projection of the spiral cords.

Hypotype: MPEF-PI-135; length: 14 mm; width: 12 mm.

Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Discussion: The unique example found has been replaced totally with gypsum, but the conchological characters are well preserved, and we consider that it resembles the species *Buccinulum (Glypteuthria) agnesia* (Strebel, 1905), living from 35 degrees South latitude to the Magellanic region. It differs from *Buccinulum (Glypteuthria) acuminata* (E.A. Smith, 1915) by the number of axial cords (28) and by the number of spiral cords (22) on the last whorl. *Buccinulum (Glypteuthria) agnesia* is reported for the first time from the Entrerriense Formation of South America.

Superfamily CONOIDEA
Family TURRIDAE
Subfamily TURRINAE
Genus POLYSTIRA Woodring, 1928
POLYSTIRA sp.
Plate 4, figure 8

Description: Only the siphonal canal, the last whorl and part of the penultimate whorl preserved. Body whorl cylindrical, shoulder oblique, ornamented with four spiral cords, the first forming the shoulder, the three remaining joined and separated from the first; spiral and axial striations continuing over the siphonal canal. Aperture oval; siphonal canal long and very narrow; columella straight.

Hypotype: MPEF-PI-133; approximate length: 15 mm; width: 8 mm.

Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Discussion: Because of the poor preservation of the fossil, which has been extracted as a plaster cast *in situ,* we are able to deduce that it resembles *Polystira florencae* Bartsch, 1934, which lives from North Carolina to Puerto Rico and Brazil, between 20 and 120 meters of depth, on sandy-mud bottom.

Genus BELLASPIRA Conrad, 1868
BELLASPIRA sp.
Plate 4, figure 9

Description: Shell turbiniform, strong but small. Four and one-half whorls, lacking the nepionic ones. Whorls globose, with marked, deep suture. Body whorl more than twice the

responden a la proyección de los cordones concéntricos.

Hipotipo: MPEF-PI-135; largo: 14 mm; ancho: 12 mm.

Localidad: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Discusión: El único ejemplar obtenido se encuentra totalmente reemplazado en yeso, pero conserva bien los caracteres conquiológicos, por lo que consideramos se asemeja a la especie *Buccinulum (Glypteuthria) agnesia* (Strebel, 1905), viviente desde 35 grados de latitud sur hasta la región magallánica. Difiere de *Buccinulum (Glypteuthria) acuminata* (E.A. Smith, 1915) por el número de cordones axiales (28) y por el número de cordones concéntricos (22) en el último anfracto. *Buccinulum (Glypteuthria) agnesia* se menciona por primera vez para la Formación Entrerriense de Sudamérica.

Superfamilia CONOIDEA
Familia TURRIDAE
Subfamilia TURRINAE
Género POLYSTIRA Woodring, 1928
POLYSTIRA sp.
Lámina 4, figura 8

Descripción: Se conserva solo el canal sifonal, el último y parte del penúltimo anfracto. Habitáculo cilindroide, hombro oblicuo, ornamentado con cuatro cordones concéntricos, el primero formando el hombro, los tres restantes mas juntos y separados del primero; continúan estrías concéntricas y axiales sobre el canal sifonal. Abertura oval; canal sifonal largo y muy angosto; columela recta.

Hipotipo: MPEF-PI-133; largo aproximadamente: 15 mm, ancho: 8 mm.

Localidad: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Discusión: A pesar de la mala conservación del fósil que ha sido extraído previa plastificación *in situ,* podemos deducir que se asemeja a *Polystira florencae* Bartsch, 1934, que habita desde Carolina del Norte, Puerto Rico y Brasil, entre los 20 y 120 metros de profundidad, sobre fondos arenofangosos.

Género BELLASPIRA Conrad, 1868
BELLASPIRA sp.
Lámina 4, figura 9

Descripción: Concha turbiniforme, fuerte pero pequeña. Cuatro y media vueltas, falta una nepiónica. Anfractos globosos, con aparente sutura profunda. Habitáculo de más del doble

height of the spire. Broad shoulder giving rise to strong axial cords, wide at the level of the shoulder and narrowing toward the aperture, on the last whorl nine in number; the spire whorls also present the same type of ornamentation. Columella apparently straight.

Hypotype: MPEF-PI-134; length: 11 mm; width: 10.2 mm.

Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Discussion: The example described is totally decorticate; but from the form of the shell and the ornamentation, we are inclined to include it tentatively in the genus *Bellaspira* Conrad, 1868. The most recent data that we have been able to obtain with respect to specimens of this genus, is a reference by Rios (1975), who mentions *Bellaspira* sp. (num. 587, pl. 40), from Cabeledo, Paraiba, Brazil in 30 meters depth ("A. Saldanha"). The present specimen was recovered by means of a plaster cast *in situ*. We report herein the genus *Bellaspira,* for the first time from the Entrerriense Formation of South America.

de la altura de la espira. Hombro amplio del que nacen fuertes cordones axiales, anchos a nivel del hombro y angostandose hacia adelante, en el último anfracto se cuentan nueve; las vueltas de la espira también presentan el mismo tipo de ornamentación. Columela aparentemente recta.

Hipotipo: MPEF-PI-134; largo: 11 mm; ancho: 10,2 mm.

Localidad: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Discusión: El ejemplar descrito se encuentra totalmente decorticado; pero por la forma de la concha y la ornamentación, nos inclinamos a incluirlo tentativamente en el género *Bellaspira* Conrad, 1868. El último dato que hemos podido obtener respecto a especímenes de este género, es referido por Rios (1975) que menciona *Bellaspira* sp. (núm. 587, lam. 40), obtenida en Cabeledo, Paraiba, Brasil a 30 metros de profundidad ("A. Saldanha"). Este espécimen ha sido recuperado por plastificación *in situ*. Se menciona el género *Bellaspira,* en este trabajo, por primera vez para la Formación Entrerriense de Sudamérica.

Subfamily DRILLINAE
Genus DRILLIA Gray, 1883
DRILLIA BRACACCINII, n. sp.
Plate 4, figure 10

Description: Shell very small; spire short; one and one-half smooth nepionic whorls. On the first postnuclear whorl fine axial cords and four spiral cords of equal strength; on the second whorl, fine axial cords and five spiral cords of equal strength; on the third whorl, heavy axial cords and four finer spiral cords, the first forming the shoulder of the whorl; between these one fine cord only visible under x10 magnification. The axial cords at the height of the shoulder curved in an "s" before reaching the suture. Body whorl ornamented with strong axial cords, heavy and fine spiral cords and fine growth lamellae undulating between the axial cords.

Holotype: MPEF-PI-132; length: 3 mm; width: 1.2 mm (broken).

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Osvaldo Bracaccini.

Discussion: Drillia bracaccinii, n. sp., differs from *Drillia santacruzensis* Ortmann, 1900, which has a concave band at the level of the suture, axial ornamentation only, and a callosity at the level of the posterior margin of the inner lip. *Drillia detecta* (Dall, 1881) has heavier axial cords,

Subfamilia DRILLINAE
Género DRILLIA Gray, 1883
DRILLIA BRACACCINII, n. sp.
Lámina 4, figura 10

Descripción: Concha muy pequeña; espira corta; una y media vueltas nepiónicas lisas. En la primera vuelta postnuclear se observan finos cordones axiales y cuatro concéntricos de igual espesor; en la segunda vuelta, finos cordones axiales y cinco concéntricos de igual espesor; en la tercera vuelta, gruesos cordones axiales y cuatro más finos concéntricos, el primero forma el hombro del anfracto; entre ellos un fino cordón solo visible a la lupa x10. Los cordones axiales a la altura del hombro se curvan en "s" antes de llegar a la sutura. Habitáculo ornamentado con fuertes cordones axiales, cordones concéntricos gruesos y finos y finas láminas de crecimiento onduladas entre los cordones axiales.

Holotipo: MPEF-PI-132; largo: 3 mm; ancho: 1,2 mm (roto).

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al extinto geólogo Dr. Osvaldo Bracaccini.

Discusión: Drillia bracaccinii, n. sp., difiere de *Drillia santacruzensis* Ortmann, 1900, por tener ésta una banda cóncava a nivel de la sutura, solo ornamentación axial y una callosidad a nivel del borde posterior del labio interno. Difiere de *Drillia detecta* (Dall, 1881), por tener ésta cor-

a larger number of spiral cords, and the shoulder of the whorls very angulate. This latter species is living in the Gulf of Mexico. *Drillia bracaccinii* is the second species of *Drillia* reported from the Tertiary of Patagonia and the first from the Entrerriense Formation of South America.

DRILLIA sp.
Plate 4, figure 11

Description: Shell turriform; long and narrow; three whorls and two and one-half nepionic whorls. Ornamentation consisting of oblique axial cords and finer spiral cords that form tubercules at the intersection of the axials.

Hypotype: MPEF-PI-131; length: 6 mm; width: 2 mm (broken).

Locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

Discussion: The state of preservation of this specimen is bad and it was extracted as a plaster cast *in situ*. The sample differs from *Drillia santacruzensis* Ortmann, 1900, which has a spiral groove at the level of the suture and only axial ornamentation. It also differs from *Drillia bracaccinii*, n. sp.

Superfamily PYRAMIDELLOIDEA
Family AMATHINIDAE
Genus ISELICA Dall, 1918
ISELICA DESSANTII, n. sp.
Plate 4, figure 12

Description: Shell small, not very strong, turbiniform, higher than wide; three and one-half whorls and one nepionic whorl. Spire generally high, but in some examples it is rather low. The body whorl is six times longer than the spire. Suture deep. Body whorl ornamented with eight flat, wide cords, corrugated by the growth lines that cross them, the same with the spaces between the cords. On the penultimate whorl there are four flat cords and fine axial striations. Aperture ovoid, wider anteriorly than posteriorly. Columellar callus thin, straight, separated from the body whorl by a very fine groove. Labrum reflected, more narrow anteriorly than posteriorly, with a smooth posterior angulation, crenulated along its entire length by the projection of the spiral cords. Umbilicus long, narrow, and deep. A small carina beginning at the lip penetrating into the umbilicus.

Holotype: MPEF-PI-165; length: 7 mm; width: 5 mm. Aperture: length 3 mm, width 2 mm.

Type locality: Puerto Pirámide, Valdés Peninsula, Chubut Province, Argentina.

dones axiales más gruesos, mayor número de cordones concéntricos y anfractos con hombros muy angulosos. Esta última especie es viviente en el Golfo de México. *Drillia bracaccinii* es la segunda especie de *Drillia* mencionada para el Terciario de Patagonia y la primera para la Formación Entrerriense de Sudamérica.

DRILLIA sp.
Lámina 4, figura 11

Descripción: Concha turriforme, larga y delgada; tres anfractos y dos y media vueltas nepiónicas. Ornamentación constituída por cordones axiales oblicuos y cordones concéntricos más finos que forman tubérculos al pasar sobre los axiales.

Hipotipo: MPEF-PI-131; largo: 6 mm; ancho: 2 mm (roto).

Localidad: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Discusión: El estado de conservación de este espécimen es malo y ha sido extraída previa plastificación *in situ*. Este ejemplar difiere de *Drillia santacruzensis* Ortmann, 1900, que posee un surco concéntrico a nivel sutural y solo ornamentación axial. Difiere también de *Drillia bracaccinii*, n. sp.

Superfamilia PYRAMIDELLOIDEA
Familia AMATHINIDAE
Género ISELICA Dall, 1918
ISELICA DESSANTII, n. sp.
Lámina 4, figura 12

Descripción: Concha pequeña, no muy fuerte, turbiniforme, más alta que ancha; tres y media vueltas y una nepiónica. Espira generalmente alta, pero en algunos ejemplares es algo más baja. El habitáculo es seis veces más largo que la espira. Sutura profunda. Habitáculo ornamentado por ocho cordones planos, anchos y rugosos por las estrías de crecimiento que los cruzan, lo mismo que los espacios entre los cordones. En el penúltimo anfracto se cuentan cuatro cordones planos y finas estrias axiales. Abertura ovoidea, más ancha adelante que atrás. Callo columelar fino, recto, separado del habitáculo por un finísimo surco. Labro reflejado, más ancho anterior que posteriormente, con leve angulación posterior, crenulado en toda su extensión por la proyección de los cordones concéntricos. Ombligo largo, angosto y profundo. Una pequeña carena que nace del labro penetra en el ombligo.

Holotipo: MPEF-PI-165; largo: 7 mm; ancho: 5 mm. Abertura: largo 3 mm, ancho 2 mm.

Localidad tipo: Puerto Pirámide, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Raul N. Dessanti.

Discussion: Iselica dessantii, n. sp., differs from *Iselica anomala* (C.B. Adams, 1850), which has a subcircular aperture, where the former is ovoid; width/height index of the aperture 0.66 and 0.72 for the former; a columellar callus not covering the umbilicus; it also has a strong posterior angulation of the callus and lacks the internal tubercule. Ihering (1907) reported from the Superpatagoniense of Yegua Quemada *Fossarus pilula* Cossmann, 1899, which almost surely is referable to *Iselica. Fossarus pilula* differs from *Iselica dessantii* by having eight spiral cords, the interstices between the cords of the same width as the cords, and a columellar groove that divides the columella into an internal and an external margin. Figueiras and Broggi (1971-73) reported *Iselica anomala* from the Camacho Formation (Entrerriense) of Uruguay, attributing the example with doubt to this species. The genus *Iselica* Dall, 1918, is reported for the first time herein from the Entrerriense Formation of Argentina.

Derivatio nominis: Dedicado al extinto geólogo Dr. Raul N. Dessanti.

Discusión: Iselica dessantii, n. sp., difiere de *Iselica anomala* (C.B. Adams, 1850) por tener abertura semicircular, ovoide para la primera; índice ancho/alto de la abertura 0,66 y 0,72 para la primera; callo columelar que no cubre el ombligo; fuerte angulación posterior del callo y ausencia del tubérculo interno. Ihering (1907) describe para la Formación Superpatagoniense de Yegua Quemada *Fossarus pilula* Cossmann, 1899, que casi seguramente se trate de una *Iselica. Fossarus pilula* difiere de *Iselica dessantii* por tener ocho cordones concéntricos, los intersticios entre los cordones del mismo ancho que estos, y un surco columelar que divide en un borde interno y otro externo a la columela. Figueiras y Broggi (1971-73) mencionan *Iselica anomala* para la Formación Camacho (= Entrerriense) del Uruguay, atribuyendo el ejemplar con dudas a esa especie. Se menciona por primera vez en éste trabajo el género *Iselica* Dall, 1918, para la Formación Entrerriense de la Argentina.

Class SCAPHOPODA
Order DENTALIIDA
Family DENTALIIDAE Gray, 1847
Genus DENTALIUM Linné, 1758
DENTALIUM IHERINGI, n. sp.
Plate 5, figure 1

Description: Shell slightly curved, with nine primary longitudinal ribs, low and angled; only two secondary ribs intercalated. On anterior third, principal ribs degenerate into a smoother surface. Interspaces flat and three times width of ribs.

Holotype: MPEF-PI-074; length: 19 mm; diameter: 2.2 mm; arc: 1 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to Dr. Herman von Ihering.

Discussion: The new species differs from *Dentalium sulcosum* Sowerby, 1846, in that it is smaller, has only nine costae, and these are angled. It differs from *Dentalium rebeccaense* Henderson, 1920, which has a clearly hexagonal shell and only six strong, rounded axial ribs.

Clase SCAPHOPODA
Orden DENTALIIDA
Familia DENTALIIDAE Gray, 1847
Género DENTALIUM Linne, 1758
DENTALIUM IHERINGI, n. sp.
Lámina 5, figura 1

Descripción: Concha ligeramente curvada, con nueve costillas primarias longitudinales, bajas y angulosas; solo dos costillas secundarias intercaladas. En el tercio anterior, las costillas principales se pierden en una superficie más bien lisa. Los interespacios son planos y tienen tres veces el ancho de las costillas.

Holotipo: MPEF-PI-074; largo: 19 mm; diámetro: 2,2 mm; arco: 1 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al Dr. Herman von Ihering.

Discusión: La nueva especie difiere de *Dentalium sulcosum* Sowerby, 1846, por ser más pequeña, tener solo nueve costillas y ser estas angulosas. Difiere de *Dentalium rebeccaense* Henderson, 1920, por tener ésta una conchilla claramente hexagonal y solo seis fuertes y redondeadas costillas axiales.

DENTALIUM PARDELENSIS, n. sp.
Plate 5, figure 2

Description: Shell moderately curved, slowly increasing in diameter; 12 principal ribs, slightly elevated, doubling on the anterior third of the shell; rounded and low. Interspaces very narrow, only one secondary rib. Both extremes rounded.

Holotype: MPEF-PI-075; length: 27 mm; diameter: 2.5 mm; arc: 1.5 mm.

Type locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the place of origin.

Discussion: This new species differs from *Dentalium majus* Sowerby, 1846, a fossil of the lower Patagoniense, which lacks the doubled ribs and has stronger primary and secondary ribs. It differs from *Dentalium laqueatum regulare* Henderson, 1920, because the 12 ribs of this species are prominent and without modification, presenting a typical fine reticulation. *Dentalium carduus* Dall, 1889, is compressed dorso-ventrally, has 16 narrow longitudinal ribs and the entire surface of the shell covered by elevated transverse riblets.

DENTALIUM PRUDENS, n. sp.
Plate 5, figure 3

Description: Shell gently curved, slowly increasing in diameter; 12 principal ribs, angled and elevated. Intercostal spaces fairly concave and no secondary ribs. Both extremes rounded.

Holotype: MPEF-PI-076; length: 20.5 mm; diameter: 2 mm; arc: 1.1 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: So named for having been considered a doubtful species.

Discussion: This new species differs from *Dentalium patagonicum* var. *juliana* Ihering, 1907, a fossil of the Superpatagoniense Formation, which has secondary ribs. *Dentalium laqueatum* Verrill, 1885, has secondary ribs and a fine reticulated sculpture. *Dentalium laqueatum regulare* Henderson, 1920, has a reticulated sculpture and prominent, rounded ribs.

DENTALIUM PERSEVERATUM, n. sp.
Plate 5, figure 4

DENTALIUM PARDELENSIS, n. sp.
Lámina 5, figura 2

Descripción: Concha moderadamente curva, aumentando lentamente en diámetro; 12 costillas principales ligeramente elevadas y dobles en el tercio anterior de la concha; redondeadas y bajas. Los interespacios son muy angostos, se observa solo una costilla secundaria. Ambos extremos son redondeados.

Holotipo: MPEF-PI-075; largo: 27 mm; diámetro: 2,5 mm; arco: 1,5 mm.

Localidad tipo: Punta Pardela, Península Valdés, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por su lugar de origen.

Discusión: Esta nueva especie difiere de *Dentalium majus* Sowerby, 1846, fósil del Patagoniense Inferior, por carecer ésta de costillas dobles y tener fuertes costillas primarias y secundarias. Difiere de *Dentalium laqueatum regulare* Henderson, 1920, porque las 12 costillas de ésta especie son prominentes y sin modificaciones, presentando un fino y típico reticulado. Difiere de *Dentalium carduus* Dall, 1889, por ser ésta comprimida dorsoventralmente, tener 16 angostas costillas longitudinales y toda la superficie de la concha cubierta por elevadas costulaciones transversales.

DENTALIUM PRUDENS, n. sp.
Lámina 5, figura 3

Descripción: Concha suavemente curva, creciendo lentamente en diámetro; 12 costillas principales, angulosas y elevadas. Espacios intercostales debilmente cóncavos, sin costillas secundarias. Ambos extremos redondos.

Holotipo: MPEF-PI-076; largo: 20,5 mm; diámetro: 2 mm; arco: 1,1 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por haberlo considerado una especie dudosa.

Discusión: Esta nueva especie difiere de *Dentalium patagonicum* var. *juliana* Ihering, 1907, fósil de la Formación Superpatagoniense, el cual tiene costillas secundarias. Difiere de *Dentalium laqueatum* Verrill, 1885, el cual posee costillas secundarias y una fina escultura reticulada. Difiere de *Dentalium laqueatum regulare* Henderson, 1920, el cual tiene escultura reticulada y prominentes costillas axiales redondeadas.

DENTALIUM PERSEVERATUM, n. sp.
Lámina 5, figura 4

Description: Shell long and slightly curved, mostly in the posterior third; evenly increasing in diameter; ten longitudinal rounded ribs; intercostal spaces equal in width to ribs. Secondary ribs number eight, lower and finer than primaries. Entire surface covered by transverse riblets, with appearance of circular lamellae crossing longitudinal ribs. No apical notch.

Holotype: MPEF-PI-077; length: 18 mm; diameter: 2.1 mm; arc: 1 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: So named because of the difficulty in finding a complete example.

Discussion: The new species differs from *Dentalium sulcosum* Sowerby, 1846, which has 14 primary ribs, having the costae twice the width of the intercostal spaces, and no secondary ribs. *Dentalium patagonicum* Rochebrune and Mabille, 1889, has 14 to 15 primary ribs and the secondary ribs assuming the importance of the primaries. *Dentalium carduus* Dall, 1889, has 16 longitudinal ribs and an apical notch.

DENTALIUM MAGNUMCOSTATUM, n. sp.
Plate 5, figure 5

Descripción: Concha larga y suavemente curvada, comunmente en el tercio posterior; apenas creciendo en diámetro; diez costillas longitudinales redondeadas; los espacios intercostales del mismo ancho que las costillas. Costillas secundarias en número de ocho, bajas y más finas que las primarias. La totalidad de la superficie está cubierta por costulaciones transversales con el aspecto de lamelas circulares que cruzan las costillas longitudinales. Sin muesca apical.

Holotipo: MPEF-PI-077; largo: 18 mm; diámetro: 2,1 mm; arco: 1 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por la dificultad de encontrar un ejemplar completo.

Discusión: La nueva especie difiere de *Dentalium sulcosum* Sowerby, 1846, el cual tiene 14 costillas primarias que tienen dos veces el ancho de los espacios intercostales y no tiene ninguna costilla secundaria. Difiere de *Dentalium patagonicum* Rochebrune y Mabille, 1889, el cual tiene de 14 a 15 costillas primarias y las secundarias que asumen la misma importancia que las primarias. Difiere de *Dentalium carduus* Dall, 1889, el cual tiene 16 costillas longitudinales y muesca apical.

DENTALIUM MAGNUMCOSTATUM, n. sp.
Lámina 5, figura 5

PLATE 5

Figure Page
1. DENTALIUM IHERINGI, n. sp. 48
MPEF-PI-074 (holotype); length: 19 mm; diameter: 2.2 mm; arc: 1 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
2. DENTALIUM PARDELENSIS, n. sp. 49
MPEF-PI-075 (holotype); length: 27 mm; diameter: 2.5 mm; arc: 1.5 mm.
Locality: Punta Pardela, Valdés Peninsula, Chubut Province, Argentina.
3. DENTALIUM PRUDENS, n. sp. 49
MPEF-PI-076 (holotype); length: 20.5 mm; diameter: 2 mm; arc: 1.1 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
4. DENTALIUM PERSEVERATUM, n. sp. 49
MPEF-PI-077 (holotype); length: 18 mm; diameter: 2.1 mm; arc: 1 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
5. DENTALIUM MAGNUMCOSTATUM, n. sp. 50
MPEF-PI-078 (holotype); length: 17 mm; diameter: 2.9 mm; arc: 0.8 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
6. DENTALIUM SUPERBUS, n. sp. 52
MPEF-PI-079 (holotype); length: 14.4 mm; diameter: 2.2 mm; arc: 1 mm (apex broken).
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

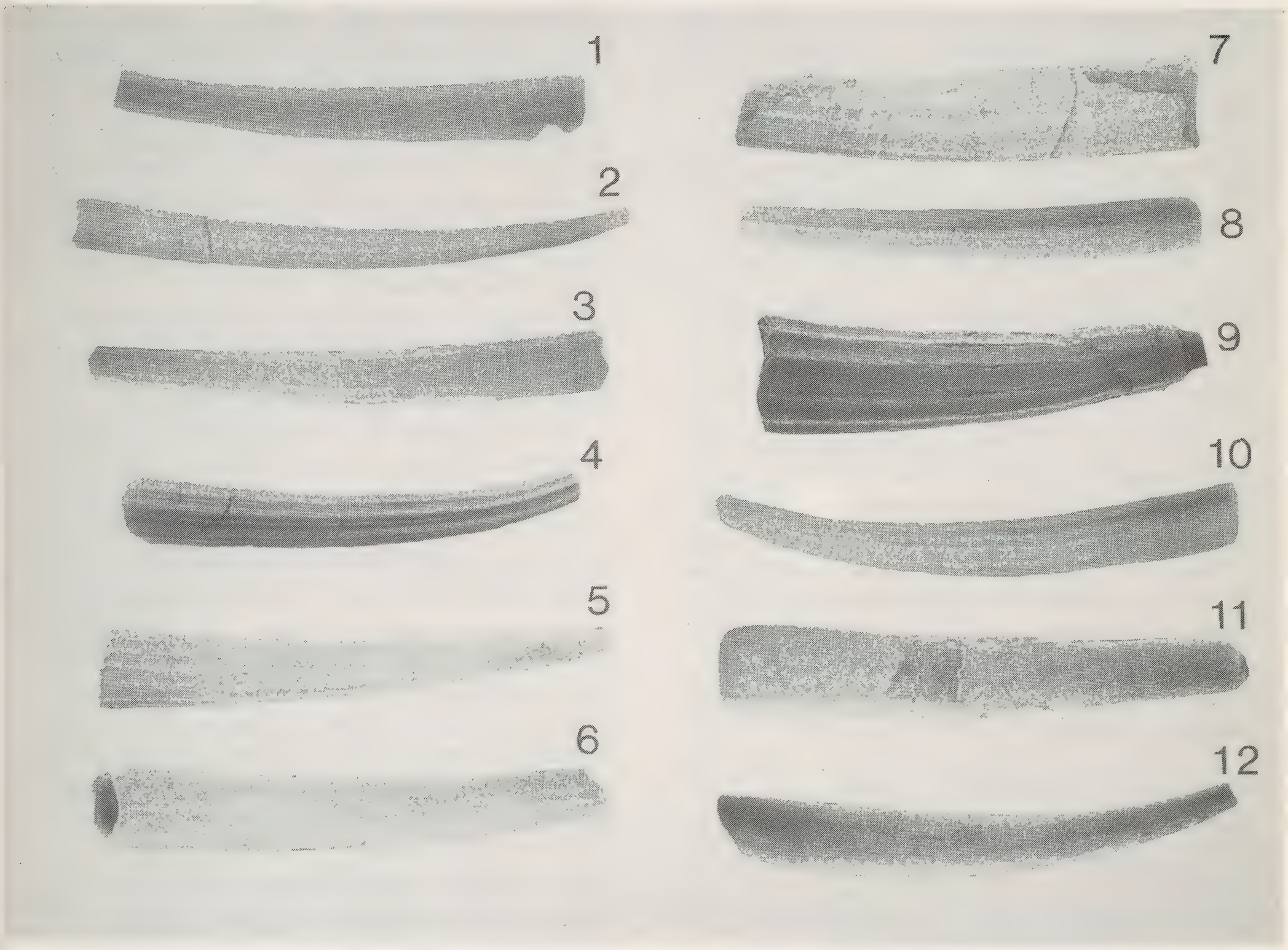

PLATE 5

7. DENTALIUM ASPERUM, n. sp. 53
MPEF-PI-080 (holotype); length: 13.5 mm; diameter: 3 mm; arc: unknown (shell broken).
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
8. ANTALIS FLECHENSIS, n. sp. 53
MPEF-PI-081 (holotype); length: 22.7 mm; diameter: 2.5 mm; arc: 0.6 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
9. ANTALIS DODECACOSTATUM, n. sp. 54
MPEF-PI-083 (holotype); length: 8 mm; diameter: 2 mm; arc: unknown (shell broken).
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
10. COCCODENTALIUM sp. 54
MPEF-PI-084 (hypotype); length: 21 mm; diameter: 2.5 mm; arc: 1.1 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
11. LAEVIDENTALIUM FERUGLIOI, n. sp. 55
MPEF-PI-060 (holotype); length: 17 mm; diameter: 3 mm; arc: unknown (broken).
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
12. DISCHIDES PATAGONICUM, n. sp. 55
MPEF-PI-082 (holotype); length: 8.9 mm; diameter: 1.1 mm; arc: 0.4 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Description: Shell long and moderately curved, hardly increasing in diameter; 14 longitudinal ribs, high and strongly angled, separated by wide concave spaces. Entire surface covered by elevated transverse riblets, with appearance of circular lamellae crossing longitudinal ribs and producing a rasp-like surface. Apex tumid by abnormal growth. No apical notch.

Holotype: MPEF-PI-078; length: 17 mm; diameter: 2.9 mm; arc: 0.8 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named thus for the strong ribs.

Discussion: This new species is readily distinguished from *Dentalium sulcosum* Sowerby, 1846, by its size, the strongly angled ribs and the absence of transverse sculpture. *Dentalium patagonicum* Rochebrune and Mabille, 1889, differs by the absence of secondary ribs and the presence of circular sculpture. *Dentalium carduus* Dall, 1889, has 16 narrow ribs and has secondary costae.

Descripción: Concha larga y moderadamente curvada, apenas creciendo en diámetro; 14 costillas longitudinales, altas y fuertemente anguladas, separadas por anchos espacios cóncavos. Superficie totalmente cubierta por elevadas costulaciones, con apariencia de lamelas circulares que cruzan a las costillas longitudinales, dando el aspecto de una superficie áspera. Apice hinchado por crecimiento anormal. Sin muesca apical.

Holotipo: MPEF-PI-078; largo: 17 mm; diámetro: 2,9 mm; arco: 0,8 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por sus fuertes costillas.

Discusión: Esta nueva especie es realmente distinguible de *Dentalium sulcosum* Sowerby, 1846, por su tamaño, las fuertes y angulosas costillas y la ausencia de escultura transversal. Difiere de *Dentalium patagonicum* Rochebrune y Mabille, 1889, por la ausencia de costillas secundarias y la presencia de escultura circular. Difiere de *Dentalium carduus* Dall, 1889, el cual tiene 16 angostas costillas y costillas secundarias.

DENTALIUM SUPERBUS, n. sp.
Plate 5, figure 6

Description: Shell moderately curved, gradually increasing in diameter; 11 rounded primary longitudinal ribs. Intercostal spaces with one or two intercalated secondary ribs; some beginning at apex, others from last third; these ribs are lower and finer than the primaries. No apical notch. Both extremes rounded.

Holotype: MPEF-PI-079; length: 14.4 mm; diameter: 2.2 mm; arc: 1 mm (apex broken).

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named thus for being the species of which the most specimens has been collected.

Discussion: The new species differs from *Dentalium (Dentalium) bothrum* Woodring, 1973, which possesses eight high primary ribs, rapidly increasing secondaries and some tertiaries, attaining a total number of 28. *Dentalium (Dentalium) armillarum armillarum* Toula, 1911, differs in having six principal ribs, but the secondaries appear very near the apical end, with as many as 12 secondaries in the intercostal spaces, whereby the distal extreme becomes circular. *Dentalium callithrix*

DENTALIUM SUPERBUS, n. sp.
Lámina 5, figura 6

Descripción: Concha moderadamente curva, creciendo gradualmente en diámetro; 11 costillas primarias longitudinales y redondeadas. Espacios intercostales con una o dos costillas secundarias intercaladas; algunas comenzando desde el ápice, otras en el tercio inferior; estas costillas son más bajas y más finas que las primarias. Sin muesca apical. Ambos extremos redondeados.

Holotipo: MPEF-PI-079; largo: 14,4 mm; diámetro: 2,2 mm; arco: 1 mm (ápice roto).

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por ser la especie de la que más ejemplares se ha obtenido.

Discusión: La nueva especie difiere de *Dentalium (Dentalium) bothrum* Woodring, 1973, el cual posee ocho altas costillas primarias, incrementándose rápidamente las secundarias y algunas terciarias, alcanzando en total un número de 28. Difiere de *Dentalium (Dentalium) armillarum armillarum* Toula, 1911, que posee seis costillas principales, pero las secundarias aparecen muy cerca del extremo apical, contándose hasta doce secundarias en los espacios intercostales, por lo que el extremo distal

Dall, 1889, differs by being strongly curved, slightly compressed laterally, with the oral aperture oval, and with a fairly long slit at the apical extreme.

DENTALIUM ASPERUM, n. sp.
Plate 5, figure 7

Description: Shell gently curved, solid. Sculpture consisting of 11 high, broad, rounded ribs. Intercostal spaces slightly concave, with same width as costae. No secondary ribs; irregular growth riblets only additional sculpture.

Holotype: MPEF-PI-080; length: 13.5 mm; diameter: 3 mm; arc: unknown (shell broken).

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named thus for the rough texture.

Discussion: The new species is distinguished from *Dentalium sulcosum* Sowerby, 1846, by its small size and the number of ribs. *Dentalium patagonicum* Rochebrune and Mabille, 1889, differs by having 14 to 15 angled ribs, and a few intercostal ribs. It differs from *Dentalium octocostatum* Ihering, 1907, by the number of primary ribs (eight) and the absence of spiral growth lines. *Dentalium texasianum* Philippi, 1848, has only six primary and a few secondary ribs.

Genus ANTALIS
H. Adams and A. Adams, 1845
ANTALIS FLECHENSIS, n. sp.
Plate 5, figure 8

Description: Shell moderately curved; ten primary rounded ribs. Five low and narrow secondary ribs. Ribs disappearing entirely on anterior third of shell, with appearance of rough surface formed by the growth lines. Apex rounded and filled with a solid plug with central orifice.

Holotype: MPEF-PI-081; length: 22.7 mm; diameter: 2.5 mm; arc: 0.6 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named thus for the place of origin.

Discussion: There are no fossil species

termina siendo circular. Difiere de *Dentalium callithrix* Dall, 1889, por ser ésta fuertemente curvada, ligeramente comprimida lateralmente, con la abertura ovalada y una larga hendidura en el extremo apical.

DENTALIUM ASPERUM, n. sp.
Lámina 5, figura 7

Descripción: Concha suavemente curvada, sólida. La escultura consiste en 11 altas, anchas y redondeadas costillas axiales. Los espacios intercostales son levemente concavos, del mismo ancho que las costillas. Sin costillas secundarias; solo estrías de crecimiento irregulares como escultura adicional.

Holotipo: MPEF-PI-080; largo: 13,5 mm; diámetro: 3 mm; arco: desconocido (concha rota).

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por su textura aspera.

Discusión: La nueva especie se distingue de *Dentalium sulcosum* Sowerby, 1846, por su pequeño tamaño y el número de costillas. Difiere de *Dentalium patagonicum* Rochebrune y Mabille, 1889, por que ésta tiene 14 a 15 costillas angulosas y algunas costillas secundarias. Difiere de *Dentalium octocostatum* Ihering, 1907, por el número de costillas primarias (ocho) y la ausencia de líneas de crecimiento concéntricas. Difiere de *Dentalium texasianum* Philippi, 1848, porque ésta tiene solo seis costillas primarias y algunas secundarias.

Género ANTALIS
H. Adams and A. Adams, 1845
ANTALIS FLECHENSIS, n. sp.
Lámina 5, figura 8

Descripción: Concha moderadamente curva; diez costillas primarias redondeadas. Cinco costillas secundarias bajas y angostas. Las costillas desaparecen totalmente en el tercio anterior de la concha, con la apariencia de una superficie áspera, formada por las líneas de crecimiento. Apice redondo y obturado con un sólido tapón con orificio central.

Holotipo: MPEF-PI-081; largo: 22,7 mm; diámetro: 2,5 mm; arco: 0,6 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por el lugar de origen.

Discusión: No existen especies fósiles

of this genus described for the Tertiary of Patagonia. The new species differs from *Antalis ceratum* (Dall, 1881) because the latter has an intercostal microscopic reticulation and angles forming nine primary ribs, separated by wide, flat, intercostal spaces. *Antalis ceratum tenax* (Henderson, 1920) has nine primary ribs increasing to between 12 and 24, and a delicate intercostal network.

ANTALIS DODECACOSTATUM, n. sp.
Plate 5, figure 9

Description: Shell moderately and rather evenly curved; 12 primary ribs rounded and rather low. Intercostal spaces faintly concave, without secondary ribs, width of intercostal spaces twice that of ribs. Apex with projecting "pipe."

Holotype: MPEF-PI-083; length: 8 mm; diameter: 2 mm; arc: unknown (shell broken).

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: So named for the number of ribs.

Discussion: There are no fossil species of this genus described for the Tertiary of Patagonia. *Antalis antillarum* (d'Orbigny, 1846) has nine primary ribs increasing by intercalation of twelve, and a wide shallow apical notch is present on the convex side.

Genus COCCODENTALIUM Sacco, 1896
COCCODENTALIUM sp.
Plate 5, figure 10

Description: Shell rather thick, strong and gently curved. Sculpture consisting of 14 primary, strongly granulose longitudinal ribs. Intercostal spaces smooth, slightly convex and differing in their width. Apex rounded and with a small internal "pipe;" coarse and irregular growth lines more or less visible over entire surface.

Hypotype: MPEF-PI-084; length: 21 mm; diameter: 2.5 mm; arc: 1.1 mm.

Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Discussion: As the shell is not well preserved, after a conscientious microscopic examination we tentatively assign this specimen to the genus *Coccodentalium* Sacco, 1896.

descriptas de éste género para el Terciario de Patagonia. La nueva especie difiere de *Antalis ceratum* (Dall, 1881), porque ésta última posee una reticulación microscópica intercostal y angulaciones formando nueve costillas primarias, separadas por anchos y planos espacios intercostales. Difiere de *Antalis ceratum tenax* (Henderson, 1920), por tener ésta nueve costillas primarias, incrementadas entre 12 y 24 y una delicada trama intercostal.

ANTALIS DODECACOSTATUM, n. sp.
Lámina 5, figura 9

Descripción: Concha moderadamente curva; 12 costillas primarias, redondeadas y más bien bajas. Espacios intercostales levemente cóncavos, sin costillas secundarias, el ancho de los espacios intercostales es el doble del de las costillas. Apice con una "pipa" prominente.

Holotipo: MPEF-PI-083; largo: 8 mm; diámetro: 2 mm; arco: desconocido (concha incompleta).

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por el número de costillas.

Discusión: No existen especies fósiles descriptas para ésta género en el Terciario de Patagonia. La nueva especie difiere de *Antalis antillarum* (d'Orbigny, 1846), porque ésta tiene nueve costillas primarias, incrementadas por la intercalación de 12 y una profunda muesca apical en el lado convexo de la concha.

Género COCCODENTALIUM Sacco, 1896
COCCODENTALIUM sp.
Lámina 5, figura 10

Descripción: Concha más bien gruesa, fuerte y sumamente curvada. La escultura consiste en 14 costillas primarias, fuertemente granulosas. Espacios intercostales lisos, levemente convexos y diferentes en su ancho. Apex redondo, con una pequeña "pipa" interna; gruesas e irregulares lineas de crecimento, más o menos visibles, sobre la totalidad de la superficie.

Hipotipo: MPEF-PI-084; largo: 21 mm; diámetro: 2,5 mm; arco: 1,1 mm.

Localidad: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Discusión: Como la concha no se encuentra bien conservada, luego de un concienzudo exámen microscópico asignamos este espécimen tentativamente al género *Coccodentalium* Sacco, 1896.

Family LAEVIDENTALIIDAE
Genus LAEVIDENTALIUM Cossmann, 1888

LAEVIDENTALIUM FERUGLIOI, n. sp.
Plate 5, figure 11

Description: Shell moderately curved, rather slender, thin but strong; with a circular aperture. Sculptureless, save for occasional circular growth lines. Impossible to know its length and whether it had an apical slit or notch because it is broken at the apex; but to judge by diameter, it must have been much longer.

Holotype: MPEF-PI-060; length: 17 mm; diameter: 3 mm; arc: unknown (broken).

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Dedicated to Dr. Egidio Feruglio.

Discussion: This genus has not been reported from the Patagoniense, nor from the Entrerriense Formation. The new species differs from *Laevidentalium callipeplum* (Dall, 1889), which has a more curved shell, a diameter of 5 mm and is extremely long (90 mm).

Familia LAEVIDENTALIIDAE
Género LAEVIDENTALIUM Cossmann, 1888

LAEVIDENTALIUM FERUGLIOI, n. sp.
Lámina 5, figura 11

Descripción: Concha moderadamente curva, más bien delgada, fina pero fuerte, con abertura circular. No esculturada, salvo por ocasionales lineas de crecimiento circulares. Es imposible conocer su largo y si tenía surco o hendidura en el ápice, debido a que su extremo superior está roto; pero prejuzgamos, por su diámetro, que su longitud era mucho mayor.

Holotipo: MPEF-PI-060; largo: aproximadamente 17 mm; diámetro: 3 mm; arco: desconocido (concha rota).

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Dedicado al Dr. Egidio Feruglio.

Discusión: Este género no ha sido aún descrito para el Patagoniense, ni tampoco para la Formación Entrerriense. La nueva especie difiere de *Laevidentalium callipeplum* (Dall, 1889) por tener ésta una concha más curva, un diámetro de 5 mm y ser extremadamente más larga (90 mm).

Family CADULIDAE
Genus DISCHIDES Jeffreys, 1867

DISCHIDES PATAGONICUM, n. sp.
Plate 5, figure 12

Description: Shell small, slender and slightly curved; concave side rather evenly arched, also convex side, with a slight convexity at a point about one-third total distance from aperture. Aperture oblique, peristome blunt and rounded. Apex cut by two lateral slits, forming two small lobes.

Holotype: MPEF-PI-082; length: 8.9 mm; diameter: 1.1 mm; arc: 0.4 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named for the region where it is found.

Discussion: Until now this genus has not been reported for the Tertiary of Patagonia. The new species differs from *Ditrupa polita* Wood, 1842 [= *Dischides* Jeffreys, 1867], which has two deep lateral slits at its apex. It also differs from *Cadulus platensis* Henderson, 1920, and *Cadulus tetrodon* Pilsbry and Sharp, 1898, both living species of the North American coast, as the former has no slit at its apex and the latter has four lobes at its apex.

Familia CADULIDAE
Género DISCHIDES Jeffreys, 1867

DISCHIDES PATAGONICUM, n. sp.
Lámina 5, figura 12

Descripción: Concha pequeña, delgada y apenas curvada; lado cóncavo levemente arqueado, lo mismo el lado convexo, con una ligera convexidad a un tercio de la abertura anterior. Abertura oblicua, peristoma embotado y redondo. Apice cortado por dos surcos laterales, formando dos pequeños lóbulos.

Holotipo: MPEF-PI-082; largo: 8,9 mm; diámetro: 1,1 mm; arco: 0,4 mm.

Localidad tipo: Baliza Punta Flecha, Puerto Madryn, Provincia del Chubut, Argentina.

Derivatio nominis: Denominado así por la region donde fue encontrado.

Discusión: Hasta el momento este género no ha sido mencionado para el Terciario de Patagonia. La nueva especie difiere de *Ditrupa polita* Wood, 1842 [= *Dischides* Jeffreys, 1867], el cual posee dos profundos surcos laterales en su ápice. Difiere también de *Cadulus platensis* Henderson, 1920, y *Cadulus tetrodon* Pilsbry y Sharp, 1897, ambas especies vivientes en las costas de América, por no tener surcos en sus ápices y la última posee cuatro lóbulos apicales.

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Volume 28

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HUBERT C. SKINNER

and

EMILY H. VOKES

Editors.

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I. ABSTRACT

A well-preserved freshwater molluscan assemblage is documented and illustrated. The malocofauna was collected from sediment samples closely associated with mastodon ulna fragments recovered from the base of a stream-cut bank in Baton Rouge, Louisiana in 1991. Mollusks and mastodon bone were deposited in a clay sediment varying to silty clay loam, dated 21,220 ± 360 yr B.P. The mollusk assemblage is indicative of a perennial, well-vegetated, quiet, shallow water environment. Mollusks differ markedly from typical Peoria Loess mollusks. It is suggested that the clay/silty clay loam containing fossil mollusk shell and mastodon bone correlates with properties of basal zone loess reported by Miller and others (1985) as forming a transition zone between the Prairie Terrace and initial late Wisconsinan loess. Shell dates, soil traits, mollusk species, and paleoecology suggest that the excavation unit yielding a fossil mastodon ulna is part of a late Pleistocene swamp subsurface where Prairie Terrace clay combined with silts derived from reworked eolian loess as well as from probable glacial silt depositions. The fossil mollusk assemblage may be indicative of basal mixed zones in other localities.

Key Words: Aquatic Gastropods, Late Pleistocene, Soil Geochronology, Basal Peoria Loess, Mastodon Preservation

II. INTRODUCTION

Molluscan macrofossils and radiocarbon dates from the base of an exposure on the North Fork of Ward Creek, within the city limits of Baton Rouge, East Baton Rouge Parish, Louisiana, provide information on the late Wisconsinan environment in southeastern Louisiana. The site is located in NW 1/4 Section 39, Township 7S, Range 1E, at an approximate position of 30 deg. 24.9 min. N. Latitude and 91 deg. 5.5 min. W Longitude. The North Fork of Ward Creek is tributary to the Amite River (Fig. 1), which discharges into Lake Pontchartrain. However, during the late Wisconsinan, the area presently occupied by Ward Creek was incorporated within the flood-

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plain of the Mississippi River (Sibley, 1972), and the Amite River was part of an ancestral river basin, which drained into the Gulf of Mexico (Autin, 1993). Ward Creek empties into Bayou Manchac (Fig. 1), which has a history of flowing alternatively west into the Mississippi River or east into the Amite River. In 1814 Andrew Jackson dammed the entrance of Bayou Manchac into the Mississippi River for strategic purposes (Sibley, 1972).

As described by Saucier (1991), during the glacial maximum, sea-level in the Gulf of Mexico was lowered about 100 meters. The area of Baton Rouge probably represents the farthest extent upvalley of direct influence of this sea-level fall. The Baton Rouge fault, which was active in the Pleistocene, is part of an east-west trending hinge line separating an area of uplift to the north from an area of active subsidence and downwarping to the south. Saucier (1991) further states that the Lower Mississippi Valley during the glacial maximum of the late Wisconsinan was characterized by extensive systems of braided streams depositing massive amounts of glacial outwash. As glaciation waned, braided stream patterns changed to meandering stream patterns, and slow, vertical accretion occurred in interbasin and backswamp areas. Transformation to a meandering regime occurred about 12,000 B.P. at the latitude of Baton Rouge. During times of glacial waning, loess was deposited in upland regions. Loess represents silt deflated from braided stream deposits. The amount of loess deposited was enormous. For instance, Peoria Loess has a maximum thickness of 27 meters in the Natchez/Vicksburg area. This wind-blown sediment in the uplands provided a source for reworked loess in lowlands. In the interglacial preceding the glacial maximum, sediments are associated with the Prairie Complex. Saucier (1991) defines the Prairie Terrace as the youngest of four major Pleistocene interglacial fluvial morphostratigraphic units. Sedimentary sequences of the Prairie Terrace consist mostly of clay, silt, and sand. Massive backswamp-clay units up to 30 meters thick are known.

Pollen analysis by Jackson and Givens (1994) suggests that during the period of late Wisconsinan ice advance (22,000-17,000 yr B.P.), the uplands in the Tunica Hills north of Baton Rouge, in the region encompassing Bayou Sara (Fig. 1), were dominated by spruce (*Picea* sp.) forests with some oak (*Quercus* sp.) admixture. Spruce forests were similarly abundant in the central Mississippi Valley during this time period. Species poor pine forests were dominant in northwest Florida from 29,000 to 14,000 yr B.P., at which time spruce had a brief period of dominance (Watt *et al.*, 1992). Presence of pine or mixed pine/hardwood forests has been suggested for several regions of the north Gulf Coastal Plain during the glacial maximum (Delcourt and Delcourt, 1977, 1983; Watts, 1970).

At the excavation site in Baton Rouge, a lowland swamp environment is indicated by the molluscan assemblage, which includes approximately 18 in-place species. Presently, these gastropod and pelecypod species are widespread in temperate regions of North America. The macrofossils retrieved from Ward Creek excavation units consist largely of mollusk shells (chiefly freshwater gastropods and clams) and mastodon bone fragments. In addition, there are two minute bone fragments of questionable origin, fine plant residue in the lower unit, and numerous plant macrofossils in the upper unit.

III. METHODS AND MATERIALS

Mastodon bone was recovered from a 70 cm x 40 cm x 25 cm area of blue/gray clay-like sediment drying to a light tan near low water level of the North Fork of Ward Creek (Fig. 2). Sediment samples were obtained from bone matrices as well as directly above and below the fossil bone and from various positions along the exposed length of a 2 meter excavation site. Additional samples were obtained in 1995 from both the upper unit and lower unit, at locations 20 to 30 cm directly behind the previously excavated bone and from the downstream boundary. The excavation site included two units (Fig. 3), the lower depositional unit being a fossiliferous blue-gray clay/silty clay loam and the upper depositional unit being a dark brown organic rich sandy clay/loam (Fig. 3). Sediment samples were disaggregated in tap water and screened for organic/inorganic matter using a screen with 2.0 mm x 2.5

mm openings. Screened concentrate was dried at low heat to preserve the samples for future reference. Material recovered within each sample was sorted and identified. Shell recovered was separated by its condition (whole or broken). Whole shells were identified by species and enumerated. Broken shell matter from those fossil-yielding samples which indicated absence of intrusive material was sent for ^{14}C radiocarbon dating analysis (based on carbon dioxide extracted from the shell).

Four screened 1991 samples and five unscreened 1995 samples were subjected to

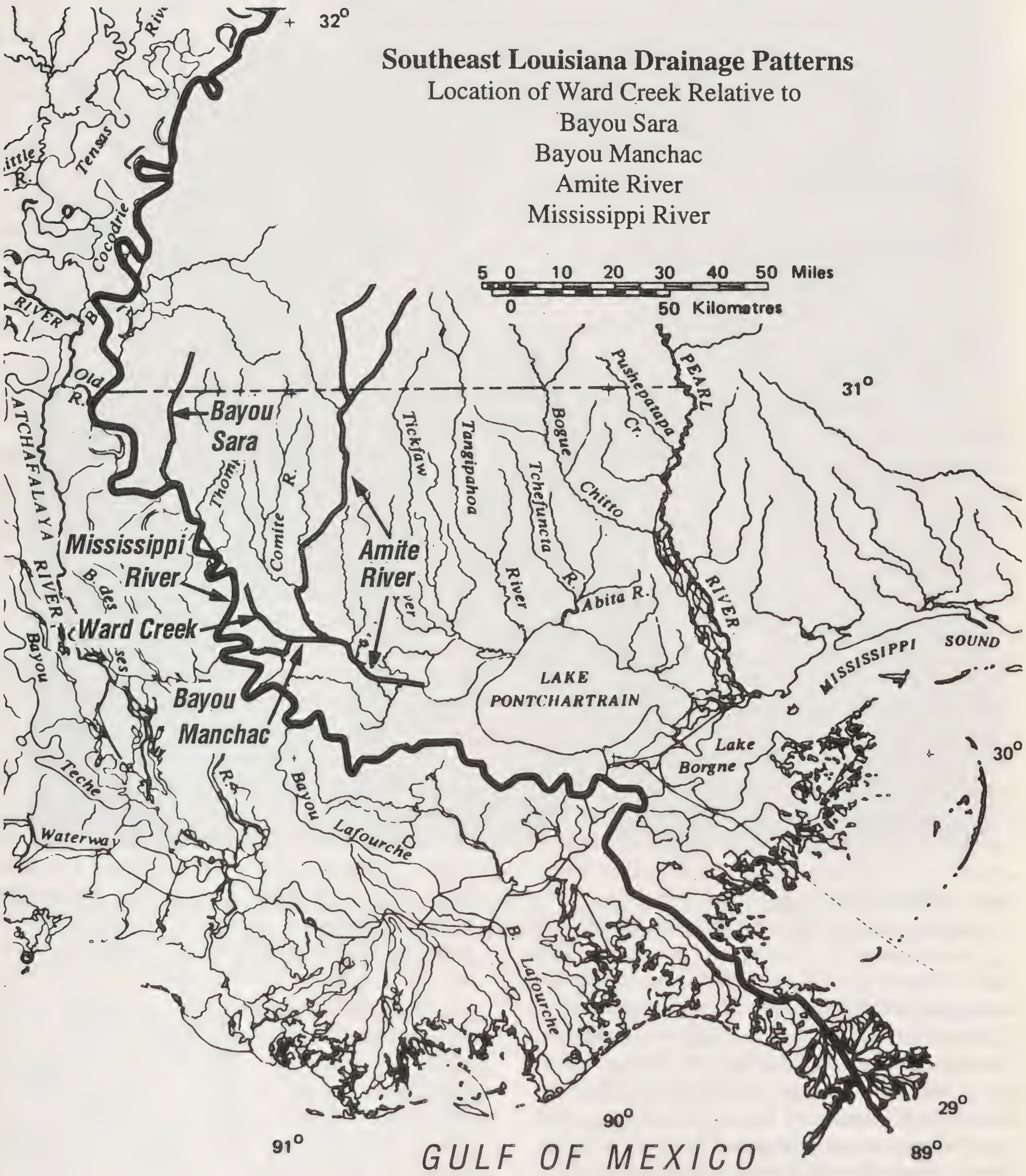


Figure 1. Location of Ward Creek relative to other southeastern Louisiana drainage systems, especially Bayou Sara, Bayou Manchac, Amite River, and Mississippi River.

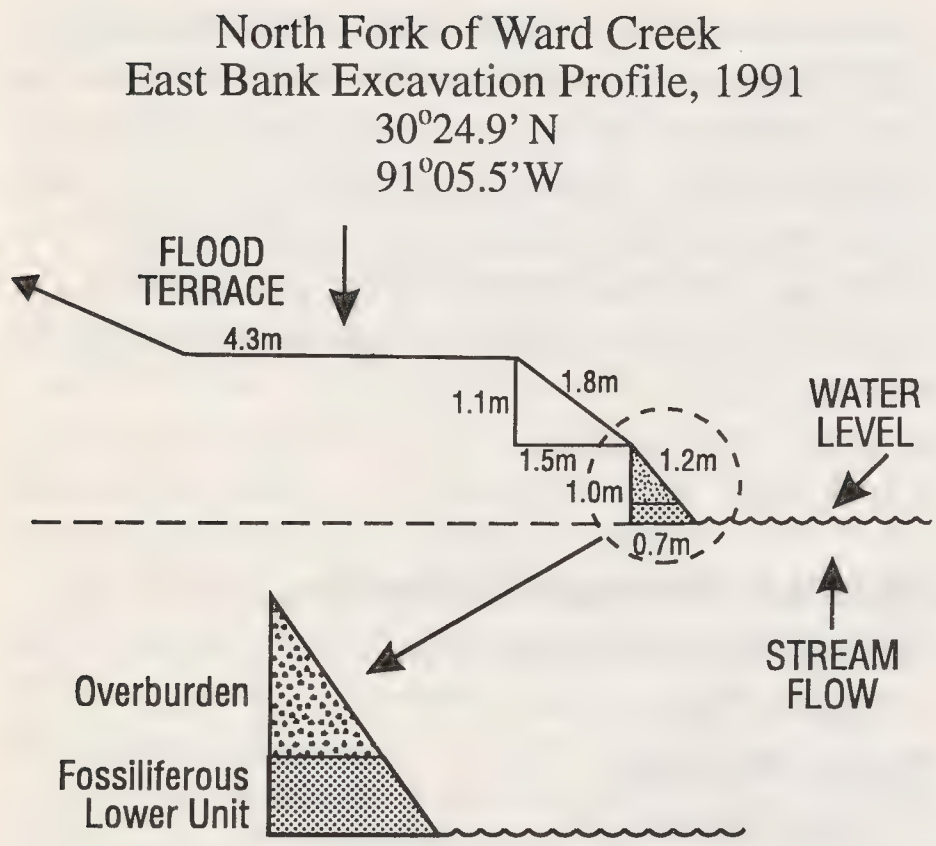


Figure 2. Diagram of the excavation profile at North Fork of Ward Creek.

granulometric analysis. These samples included six from the fossil-yielding unit, and three from the upper unit. A limited attempt was made to isolate pollen from six 1995 fossil-yielding unit samples using a scanning electron microscope and following procedures outlined by Traverse (1988) for retrieving fossil palynomorphs.

The bone matter was initially dry brushed with a soft brush and rinsed with tap water. Bone fragments were scanned under a microscope to confirm their osseous nature. A ›400 gram sample of representative smaller bone fragments was submitted to Beta Analytic Inc. of Miami, Florida for conventional ^{14}C radiocarbon analysis of bone collagen. A small sample of what appeared to be carbonized bone was submitted to Beta Analytic Inc. to ascertain its potential for dating by ^{14}C accelerated mass spectrometry (AMS) (see Stafford, 1988 or Stafford, 1990).

Large bone fragments were identified by reference to literature on mastodon bone (especially Olsen, 1979) and by use of comparative collections at Louisiana State University Museum of Natural Science, Tulane University Museum of Natural History, Dallas Museum of Natural History, Houston Museum of Natural Science, and the University of Oregon Thomas Condon State Museum of Fossils. Comparison of bone quality was made to a nearly complete mastodon skeleton (LSUMG 586) recovered from the same site in 1974 (Rice, 1981). That find is in the collection of the Louisiana State University Museum of Natural Science (formerly the LSU Museum of Geoscience).

Mollusk shells were identified by reference to descriptive and pictorial literature on mollusks. Of importance in this procedure were the following references: Andrews, 1981; Baker, 1945; Burch, 1962; Burch, 1975; Burch and Tottenham, 1980; Clarke, 1981; Dennis, 1928; Emerson and Jacobson, 1976; Jacobson and Emerson, 1961; Leonard, 1959; Richards, 1938a and 1938b, and Thompson, 1968. Turgeon *et al.* (1988) provided a source for current taxonomic nomenclature and revised common names. Specimens reported by Richards (1938a and 1938b) and curated at LSUMNS provided reference to a comparative collection.

IV. RESULTS

Bone fragments of a large mammal recovered on Oct. 18, Nov. 1 and 17, 1991 are those of the mastodon *Mammut americanum* (Kerr, 1792) of late Pleistocene age (Rancholabrean N. A. Land Mammal Age) (Olsen, 1979; Gilbert, 1990). The larger bone fragments form part of a mastodon right ulna shaft (Fig. 4). Greatest representation is of the medial midshaft, which allows a midshaft antero-posterior diameter measurement of 118 mm. Also present is a flattened anterior portion where the radius permanently crosses the ulna. The medial proximal shaft antero-posterior diameter is approximately 230 mm. Articulated fragments give a shaft length measurement of approximately 390 mm. These measurements correspond to those recorded by Olsen (1979) for similar portions of a mastodon ulna and closely match a mastodon model displayed at Houston Museum of Natural Science. However, measurements are only slightly greater than a mature juvenile mastodon ulna with partially fused epiphyses (Condon Museum 29247). The bone recovered in 1991 is comparable in quality to the bone of an adult mastodon skeleton (LSUMG 586) excavated at this site in 1974 (Rice, 1981). However, no ulna bone is described for LSUMG 586. Although reference to comparative collections at the Louisiana State University Museum of Natural Science indicates that

Figure 3. Excavation Unit at the North Fork of Ward Creek 11/17/91. Loose dark brown soil supporting vegetation (upper unit) overlays calcareous clay shelf (lower unit). Arrows point to Bone #4, enclosed within the lower unit.

young juvenile mastodon bone was recovered previously from the North Fork of Ward Creek (LSUMG 588), no young juvenile mastodon bone was recovered in 1991. Bone fragments found in close proximity to the mastodon ulna could reasonably be assigned to missing portions of the ulna. Numerous minute bone fragments were closely associated with the larger fragments in the screened samples.

Granulometric analysis of unscreened sediment adjacent to the bone indicates that the mastodon bone was enclosed in a calcareous clay/silty clay loam. Screened samples of the bone matrix indicate a silty clay loam (Table 1). The fossil-bearing unit (Fig. 3) is characterized by bleached freshwater mollusk shell, calcareous/clay concretions (especially calcareous nodules), clay aggregations, iron oxide nodules,

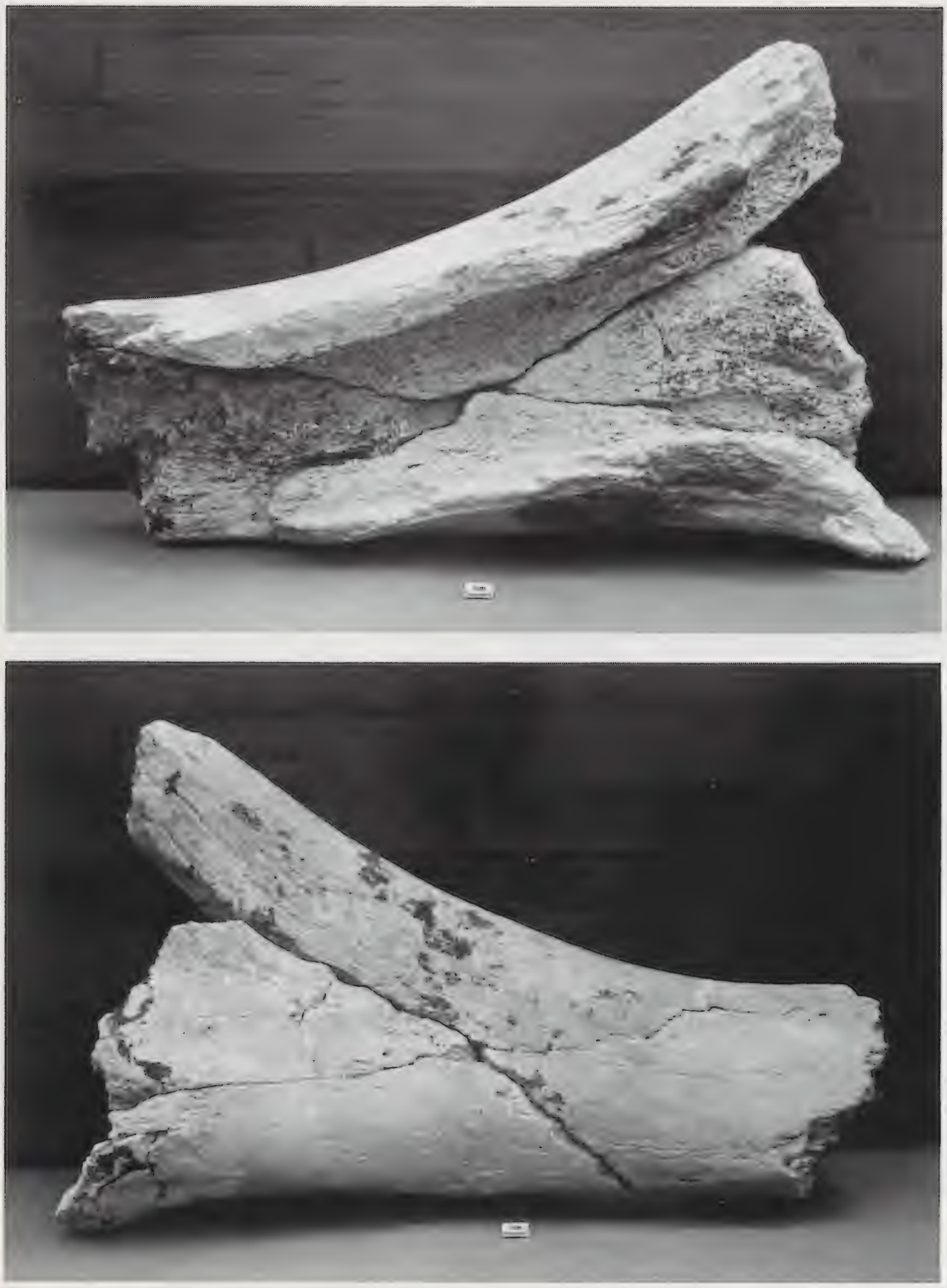


Figure 4. Composite of mastodon right ulna shaft fragments retrieved from the lower excavation unit: (a) interior view of medial shaft, (b) exterior view of medial shaft. Scale is 1 cm.

bone, and some black gravel and fine plant residue. No pollen was isolated from this unit, possibly a reflection of the high carbonate fraction (Table 1). Pollen exines are sensitive to a high pH over long periods (Traverse, 1988). In contrast, the unit overlying the fossil-bearing unit (Fig. 3) is characterized by freshwater mollusks retaining abraded periostracum, mixed gravels, quartz/agate sand, plant materials (fragments of seeds, stems, wood, leaves, and roots), and intrusive materials such as glass and plastic. Granulometric analysis of the unit overlying the fossil-yielding unit

varies from sandy clay loam to clay (Table 1). This sediment appears to be a combination of recent alluvium and colluvial slumped deposits, showing strong but varied influence of the underlying clay.

Bone collagen had been leached out or replaced by organic/inorganic components in the submitted ›400 grams of bone. Therefore, bone collagen radiocarbon dating was not feasible. An attempt to obtain a direct date from bone by using the ^{14}C AMS method on a small sample of possibly carbonized bone proved similarly fruitless.

The sediment surrounding mastodon bone fragments contained numerous fossil freshwater mollusk shells (Table 2; Figs. 5-11). A radiocarbon date of 21,220 $\pm$ 360 yr B.P. (Beta-54921, 1992) obtained from 10 grams of shell retrieved from sediment associated with the mastodon bone and the whole shell places this molluscan faunal assemblage within a late Pleistocene, late Wisconsinan time frame (22,000 to 17,000 yr B.P.). This date corroborates a date of 20,595 $\pm$ 225 yr B.P. (Beta-1854, 1979) obtained by Alford, Kolb, and Holmes from shell in this vicinity (Alford, pers. comm.). This age was corroborated later by Clark *et al.* (1989) who applied the amino acid racemization method of dating to three samples of cf. *Mesodon* sp. from the same stratigraphic unit at Ward Creek used to determine the above mentioned 20,595 $\pm$ 225 yr B.P. radiocarbon date . Clark *et al.* (1989) reported a total acid hydrolysate value of 0.16 $\pm$ 0.03 for these Ward Creek gastropods, a value which they related to overlapping ratios for Peoria Loess and Roxana Silt in the Mississippi Valley.

Although some taxonomic designations have changed (Turgeon *et al.* 1988), the species documented (Table 2) closely correspond to Pleistocene species cited by Richards (1938a) from Bayou Manchac and basal zone Peoria Loess at Little Bayou Sara. Bayou Manchac is immediately to the south of Baton Rouge. Little Bayou Sara is an upland stream bordering the Mississippi River valley in the Tunica Hills, West Feliciana Parish (Fig. 1).

Aquatic mollusks retrieved at Ward Creek are sphaeriid bivalves and gastropods represented by planorbids, hydrobiids, succineids, pomatiopsids, pyramidellids, physids, and lymnaeids. Beyond the excavation borders but within the same soil profile, there is, additionally, very limited representation of terrestrial polygyrids. Most species are presently known throughout the Mississippi Valley, ranging from Southeast Canada to Florida and Texas, and some are more generally known from temperate latitudes of North America. Several of the fossil species have been documented at other Pleistocene localities (*e.g.*, Richards, 1938a; Baker, 1945; Taylor, 1985; W. Miller, 1989). Most species are known from perennial, freshwater habitats characterized by a mud substrate and low-energy, well-vegetated, shallow water. A few are known to inhabit vegetation at the water's edge.

TABLE 1. Granulometric Analysis of Ward Creek Base Sediments.

Sample#	Sediment Type	Carbonate Fraction %	Organic Fraction %	Particle Size %		
				Sand	Silt	Clay
PLEISTOCENE BASE UNIT						
*WC-91-30b	silty clay loam	high	15.0	5.5	68.5	26.0
*WC-91-20	silty clay loam	high	20.0	4.8	60.9	34.3
WC-95-5	clay	14.34	low	9.2	39.9	50.9
WC-95-11a	silty clay loam	high	low	5.0	57.6	37.4
WC-95-11b	silty clay loam	high	low	4.8	55.8	39.4
WC-95-7	clay	7.33	low	15.5	20.1	64.4
WC-95-15	silt loam	13.00	low	31.0	58.8	10.2
HOLOCENE OVERBURDEN UNIT						
*WC-91-16	sandy clay loam	low	50.0	47.5	24.9	27.6
*WC-91-28	silty clay	low	40.0	12.5	44.3	43.2
WC-95-12	clay	0.73	high	32.3	16.6	51.1

* = pre-screened sample

TABLE 2. Mollusks (Gastropoda and Bivalvia) recovered from the 1991 Ward Creek Mastodon excavation by sediment unit: Number of Identified Specimens of represented taxa. Comparison to Louisiana Pleistocene sites* reported by Richards (1938a) is provided.

Family	Species/Common Name**	NISP***
PLEISTOCENE FOSSIL-YIELDING UNIT		
CLASS BIVALVIA		
Sphaeriidae:	*Musculium partumeium* (Say, 1822) swamp fingernailclam	1
	Pisidium sp. unidentified species	4
	Pisidium ?compressum Prime, 1852 ridged-beak peaclam Similar to *P. variabile* of Richards (1938a) LBS, BM	1
	Pisidium ?equilaterale Prime, 1852 round peaclam	1
	Pisidium ?variabile Prime, 1852 triangular peaclam Similar to *P. compressum* of Richards (1938a) LBS, BM	1
Corbiculidae:	*Corbicula fluminea* (Muller, 1774) intrusive Asian clam	1
	Total Pleistocene Unit Bivalve Specimens	9
CLASS GASTROPODA		
Hydrobiidae:	*Amnicola limosus* (Say, 1817) [some ?*Cincinnatia* sp.] mud amnicola/?siltsnail Richards (1938a) reports *Cincinnatia cincinnatiensis* LBS, BM	46
Pomatiopsidae:	*Pomatiopsis lapidaria* (Say, 1817) slender walker Similar to *P. lapidaria* of Richards (1938a) LBS, BM	10
Pyramidellidae	?*Fargoa gibbosa* (Bush, 1909) odostome	8
Lymnaeidae:	*Fossaria parva* (I. Lea, 1841) pygmy fossaria Richards (1938a) reports *Lymnaea obrussa* LBS	3
Physidae:	*Physella heterostropha* (Say, 1817), small form pewter physa Similar to *Physa gyrina elliptica* of Richards (1938a) LBS, BM	4
Planorbidae:	*Gyraulus parvus* (Say, 1817) ash gyro Similar to *G. parvus* of Richards (1938a) BM	206
	Helisoma anceps (Menke, 1830) two-ridge rams-horn Similar to *H. anceps* of Richards (1938a) LBS, BM	10
	Planorbella trivolis (Say, 1817) marsh rams-horn [*P.t. lentum* = southern subspecies]	2
	Planorbella sp. unidentified species	3
	Micromenetus alabamensis (Pilsbry, 1895) marsh sprite	4
	?*Micromenetus* sp. unidentified species	1

	?*Vorticifex* sp. ?*V. effusus* (I. Lea, 1856) [resembles the extinct *Parapholyx pusilla* Baker, 1945]	1
Succineidae:	*Succinea* sp. ?*S. forsheyi* (I. Lea, 1864) amber snail Richards (1938a) reports *Succinea* sp. LBS	7
	Total Pleistocene Unit Gastropods	305
PLEISTOCENE EXPOSED BANK		
CLASS BIVALVIA		
Corbiculidae:	*Corbicula fluminea* (Muller, 1774) intrusive Asian clam	2
	Total Exposed Bank Pleistocene Bivalves	2
CLASS GASTROPODA		
Physidae:	*Physella heterostropha* (Say, 1817), large form pewter physa Size comparable to *Physa halei* of Richards (1938a) LBS	4
Planorbidae:	*Planorbella trivolis* (Say, 1817) marsh rams-horn [*P.t. lentum* = ?Southern subspecies]	9
Polygyridae:	*Triodopsis albolabris* (Say, 1816) whitelip	1
	Mesodon sp. unidentified species	1
	Total Exposed Bank Pleistocene Gastropods	17
	TOTAL PLEISTOCENE ASSEMBLAGE BIVALVES	11
	TOTAL PLEISTOCENE ASSEMBLAGE GASTROPODS	322
	TOTAL PLEISTOCENE MOLLUSK SPECIMENS	331
HOLOCENE ALLUVIUM/COLLUVIUM		
CLASS BIVALVIA		
Sphaeriidae:	*Sphaerium striatinum* (Lamarck, 1818) striated fingernailclam	28
	Sphaerium ?fabale (Prime, 1852) river fingernailclam	1
	Musculium transversum (Say, 1829) pond fingernailclam	10
Corbiculidae:	*Corbicula fluminea* (Muller, 1774) Asian clam	4
	?*Polymesoda* sp. unidentified clam	1
	Total Holocene Bivalve Specimens	44
CLASS GASTROPODA		
Hydrobiidae:	*Amnicola limosus* (Say, 1817) [some ?*Cincinnatia* sp.] mud amnicola/?siltsnail	48
Lymnaeidae:	*Fossaria parva* (I. Lea, 1841) pygmy fossaria	3
Physidae:	*Physella heterostropha* (Say, 1817)/P. ?*gyrina* (Say, 1821) pewter physa/tadpole physa	14
Planorbidae:	*Gyraulus parvus* (Say, 1817) ?intrusive ash gyro	4
	Planorbella armigera (Say, 1821) thicklip rams-horn	1
Zonitidae:	?*Ventridens ligera* (Say, 1821) globose dome	1
	Total Holocene Gastropod Specimens	71

(Continued next page)

TOTAL HOLOCENE ASSEMBLAGE BIVALVES	44
TOTAL HOLOCENE ASSEMBLAGE GASTROPODS	71
TOTAL HOLOCENE ASSEMBLAGE MOLLUSK SPECIMENS	115

* LBS = Little Bayou Sara
BM = Bayou Manchac
** Following Turgeon *et al.*, 1988.
*** Numbers comparable only within sediment unit; enumerations representative of individuals except for the Holocene bivalves, *Sphaerium striatinum* and *Musculium transversum*.

Planorbidae is the best represented gastropod family in the Ward Creek excavation unit associated with mastodon bone. The most abundant species (206 specimens retrieved) is *Gyraulus parvus* (Fig. 5a), a small species of the lung-breathing family Planorbidae. At Ward Creek, *Gyraulus parvus* ranges in size from 1 to 4 mm in width and approximates 1.5 mm or less in height. An uncommon planorbid in this size range is *Micromenetus alabamensis* (Fig. 6a), with 4 specimens present. The shell is very small and ultradextral. A larger (approximately 7 mm width) planorbid is *Helisoma anceps* (Fig. 5b). This ultradextral bicarinate species is characterized by a prominent carina on the shoulder of the body whorl. An even larger planorbid species recovered at Ward Creek is sinistral in orientation and is identified as *Planorbella trivolis* (Fig. 7a). The larger of these specimens are 16-18 mm in width with a height of approximately 6 mm. Some also resemble *Planorbella pilsbryi*. One incomplete planorbid present resembles an extinct Pleistocene species from the western United States, recorded by Baker (1945) as *Parapholyx pusilla* (Fig. 6c), a genus now incorporated within *Vorticifex* (Turgeon *et al.*, 1988).

The gill-breathing Hydrobiidae (Fig. 8a) is the next most frequently represented gastropod family at Ward Creek. A flattened nuclear whorl and 3.5 to 4.5 body whorls identifies *Amnicola limosus* as the most common representative of hydrobiids (Clarke, 1981). Some specimens, however, resemble the siltsnail, *Cincinnatia* sp. (Thompson 1968; Burch and Tottenham, 1980). Pyramidellidae are questionably represented by *Fargoa gibbosa* (Fig. 8b), known from beach habitats.

Less frequently occurring amphibious species in the Ward Creek fossil-bearing unit are of the families Lymnaeidae (Fig. 8c), Pomatiopsidae (Fig. 9a), and Succineidae (Fig. 9b) (Leonard, 1959; Jacobson and Emerson, 1961; Burch and Tottenham, 1980; Andrews, 1981; Clarke, 1981). Characteristics of the reproductive system are utilized to distinguish species of Succineidae (Spamer and Bogan, 1993). The Ward Creek species resembles *Succinea oblonga*, known from freshwater Pleistocene mammal localities of western Europe (Tate, 1866). It is similar to *Succinea forsheyi* (formerly *Succinea concordialis*, a species previously recognized from Louisiana) (Turgeon *et al.*, 1988). Larger specimens of *Succinea* sp. are associated with another nearby mastodon skeleton, the Morgantown Mastodon from Natchez, southwestern Mississippi, which is part of the collection at LSUMNS.

Taxonomic relationships of the family Physidae are presently in a state of flux (Clarke, 1981; Turgeon *et al.*, 1988; Spamer and Bogan, 1993). Polymorphisms in *Physa* shells are more often a reflection of environmental influence than of speciation events (Emerson and Jacobson, 1976). *Physa* shells in the Ward Creek clay/silty clay loam come in two forms (Fig. 7b-c), differentiated by size and color. The larger form with a thicker, bleached pink shell is identified here as *Physella heterostropha* (large form). It resembles *Physa halei* (Richards, 1938a) and *Physa hawnii* (Leonard, 1959), species not listed by Turgeon *et al.* (1988). Clarke (1981) reports that shells of *P. integra*, a lake species, are thicker and heavier than the thin shells of *P. heterostropha* or *P. gyrina*. A small species with a bleached white thin shell is identified here as *Physella heterostropha* (small form). It resembles *Physa gyrina elliptica* (Richards, 1938a) and *Physa anatina* (Leonard, 1959). Clarke (1981) re-

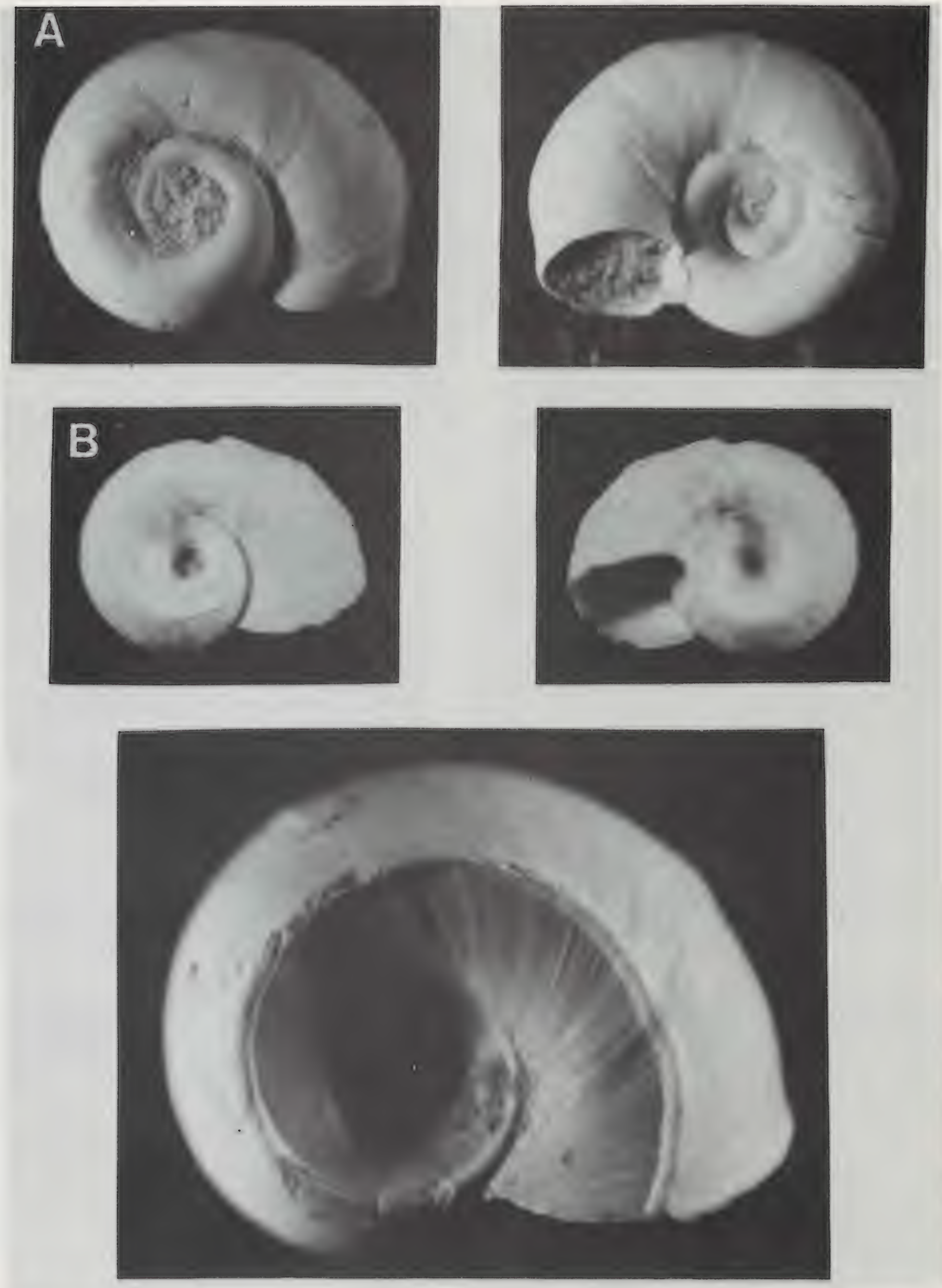


Figure 5. Ward Creek Pleistocene planorbids, apical and umbilical views: (a) *Gyraulus parvus* [x 16.7, WC-91-30b]; (b) *Helisoma anceps* [macroscopic view x 2.5, WC-91-19; (c) *Helisoma anceps* [microscopic view x 13.6, WC-91-20].

ports that *P. heterostropha* and *P. gyrina* may be more closely related than indicated by their nomenclature.

Small clams (3-4 mm) of the subfamily Pisidiinae (Fig. 10) also occur in the bone-bearing unit. *Pisidium* species (peaclams) are frequently left unidentified in fossil collection reports due to difficulties of positive identification (Burch, 1975; W. Miller, 1989). Because several species are present at Ward Creek, an attempt is made here to provisionally identify some of these species. Typical of these peaclams is *Pisidium compressum*. Other species present appear to be *P. variabile* and *P. equilaterale*. There is a single representative of the swamp fingernailclam (Fig. 11), *Musculium partumeium* (Burch, 1975; Clarke, 1981).

Just beyond the excavation site but within the fossil-yielding unit, two non-intrusive terrestrial gastropods of the family Polygyridae were recovered, *Triodopsis albolabris* and *Mesodon* sp. (Leonard, 1959; Jacobson and Emerson, 1961; Burch, 1962).

The molluscan assemblage of the sediment that overlies the bone-bearing unit at Ward Creek is distinctly different from the Pleistocene assemblage. Common to the upper unit are Sphaeriinae, Hydrobiidae and Physidae. Also present in the upper unit are the introduced bivalves of the family Corbiculidae. Lymnaeidae is represented by *Fossaria parva*. Within the upper unit, small *Physella* species retaining a thin, shiny gray/yellow periostracum are identified as *P. heterostropha*/?*gyrina*. Planorbids are rare in the upper unit. One specimen of *Planorbella armigera* was recovered (Clarke, 1981). Absence of periostracum from four specimens of *Gyraulus parvus* suggests that *G. parvus* is intrusive to the upper unit. Recall that absence of periostracum is a characteristic of the bone-bearing unit. Possible sources of contamination include reworking of soil by crawfish noted near the mastodon bone, movement of soil through degraded pipes noted at the upstream boundary, or displacement of soil by stream erosion.

V. DISCUSSION

Distribution patterns for aquatic gastropods and pelecypods of North America suggest that the Ward Creek faunal assemblage occurs over a broad latitudinal and temperature range (Burch and Tottenham, 1980; Clarke, 1981; Taylor, 1985; Spamer and Bogan, 1993). A few corresponding aquatic mollusk species have been reported for the Mammoth Site, Hot Springs, South Dakota, dated *ca.* 26,000 yr B.P. (Mead *et al.*, 1990), and from a mammoth kill-butchering locality on the edge of a late Pleistocene pond or marsh in the White River Badlands, South Dakota, *ca.* 11,000 B.P. (Hannus, 1990). Although biogeography of terrestrial snails has been used to infer paleoclimatic changes (McCraw, 1990), aquatic mollusks present at Ward Creek are not conducive to such analyses. Taylor (1985) asserts that Pleistocene aquatic habitats were not subject to the intense cyclical fluctuations characteristic of Pleistocene terrestrial habitats.

Interpretation of southeastern Louisiana paleoclimate is more accurately reflected by pollen analysis. Although fossil flora at the excavation site evidently differed from the dominant spruce forests reported for contemporaneous sites in the Tunica Hills by Givens and Givens (1987) and Jackson and Givens (1994), the proximity of these locations suggests regional influence and concordant similar though not identical paleoclimates. Jackson and Givens (1994) indicate that the Tunica Hills region of Louisiana represents the southernmost documented occurrence of widespread late Wisconsinan spruce forests and infer from pollen analysis that late Wisconsinan climate in the Tunica Hills region was cooler than present, but not boreal in nature. A slightly warmer condition is inferred for the pine or mixed pine/hardwood forests apparently typical of full-glacial vegetation of the Gulf Coastal Plain (Delcourt and Delcourt, 1977, 1983; Watts, 1970, Watts *et al.*, 1992).

A date in the range of 21,220 $\pm$ 360 yr B.P. corresponds to a time of greatest extent of the Laurentide ice sheet (Catto and Mandryk, 1990; Meltzer, 1993). The date and associated mastodon bone suggests that, like the Tunica Hills region approximately 50 kilometers to the northwest, the climate at Ward Creek was temperate but not boreal. Reasons for a cooler regional paleoclimate are related to global cooling during the late Wisconsinan glacial maxi-

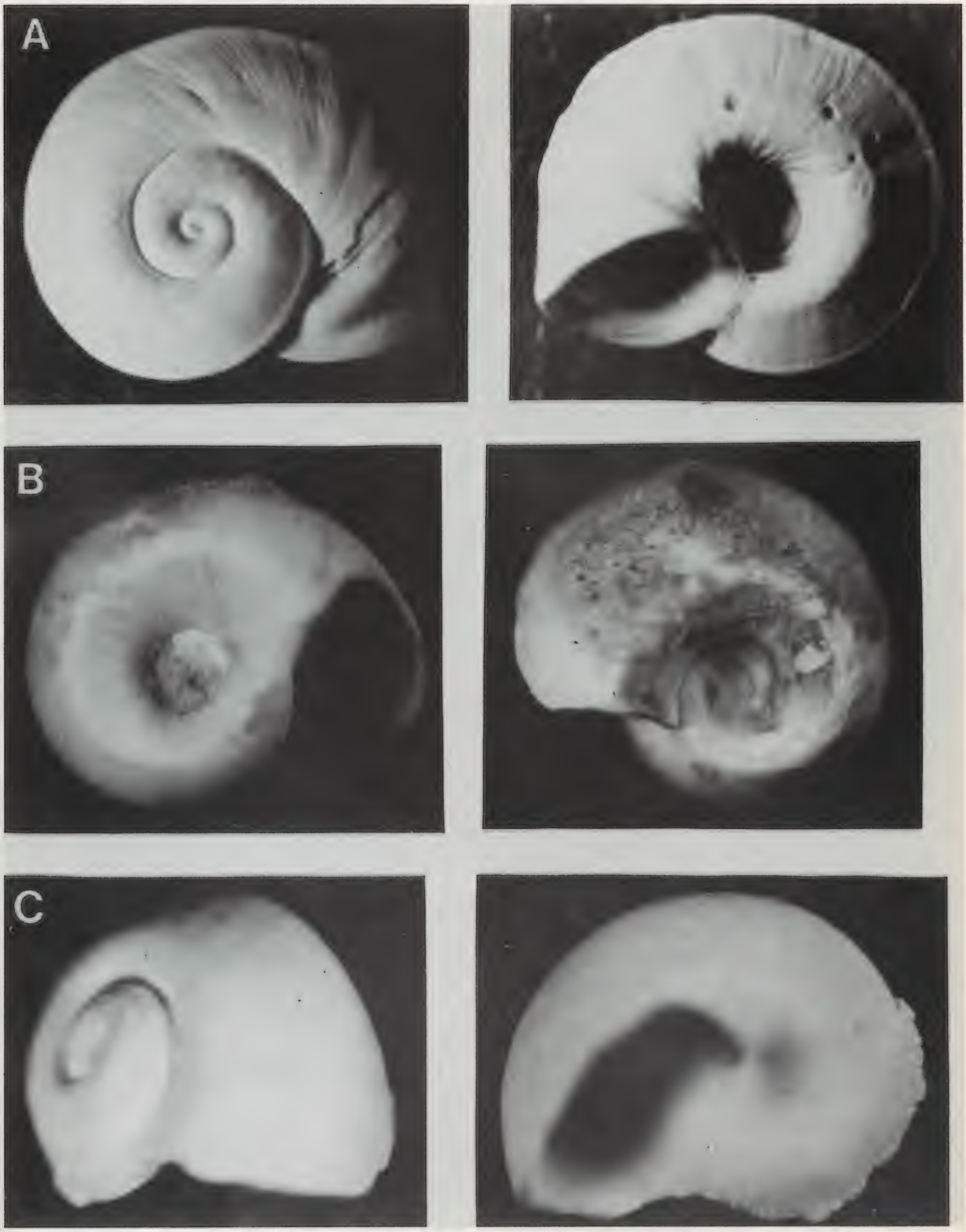


Figure 6. Ward Creek Pleistocene planorbids, apical and umbilical views: (a) *Micromenetus alabamensis* [x 13.5, WC-91-32]; (b) ?*Micromenetus* sp. [x 23.5, WC-91-19]; (c) ?*Vorticifex* sp. [x 34.2, WC-91-30c].

mum and its multiple side effects such as presence of glacial meltwater in the Mississippi Valley, low sea level, and lower than present sea level temperature.

Dates acquired from aquatic mollusks are problematic. MacDonald *et al.* (1991) report that aquatic mollusks have a tendency to take on the carbon isotope balance of lake water which tends to be deficient in ^{14}C relative to the proportion of ^{14}C in the atmosphere. Limnic sediments may reflect "old carbon" and may be several thousand years younger than radiocarbon dating indicates. However, large, shallow lakes with slow turnover of water are less prone to this error than small, deep lakes (MacDonald *et al.*, 1991). The Ward Creek mollusk assemblage suggests a shallow water environment with little movement of water.

Despite limitations on inferring paleoclimate directly from the aquatic mollusk assemblage, distribution of mollusk species through space and time can be informative. Identification of mollusk species recovered from two vertically adjacent sediment units at the excavation site provides information on the micro-paleoenvironmental history at Ward Creek. The paleoecology inferred from biostratigraphy and species composition contrasts with current ecological conditions. Within the fossil-yielding unit, the molluscan assemblage is indicative of a swamp. Most molluscan species are aquatic or amphibious, known to inhabit perennial, shallow, still-water habitats characterized by abundant vegetation and a mud substrate (Clarke, 1981). Most species, including the dominant species *Gyraulus parvus*, fall into what Taylor (1985) classifies as Group E, snails of seasonal or perennial water bodies of limited extent. However, Taylor's (1985) Groups B and C, Sphaeriidae and snails of larger perennial water bodies, are represented by *Pisidium compressum* and *Helisoma anceps*. Species recorded are not indicative of cold, clear, fast-running water (Baker, 1945).

Gastropods of the family Planorbidae are abundant in the fossil-bearing sediment. These gastropods are part of a food chain suggesting associated faunal presence of wading birds, ducks, songbirds such as red-winged blackbirds, fish, turtles, frogs, newts, salamanders, crawfish, leeches, and dragonflies (Baker, 1945).

Several of the Ward Creek species (*e.g.*, *Gyraulus parvus, Planorbella trivolis, Helisoma anceps, Pomatiopsis lapidaria, Fossaria parva*) are known intermediate hosts for blood parasites (Baker, 1945; Clarke, 1981). This suggests to the author that blood parasites were a probable environmental stress for mastodons inhabiting the Ward Creek region.

Within the Holocene upper unit, common species represent hydrobiids, physids, and freshwater sphaeriid clams (*Musculium transversum, Sphaerium striatinum,* and *Sphaerium ?fabale*), species which conform with the present Ward Creek stream habitat from which they were retrieved. Dominance of *Musculium transversum* and *Physella* sp. is sometimes associated with organic pollution and a reduced oxygen environment (Clarke, 1981). Numerous indicators of extant chemical and organic pollution are present at the Ward Creek site. Species composition supports a designation of the upper unit as recent alluvium.

Aquatic and amphibious mollusk species identified in the fossil-bearing sediment correspond closely to species identified by Richards (1938a) from Pleistocene localities in Louisiana and Mississippi such as the aquatic clay at Bayou Manchac or basal zone Peoria Loess at Little Bayou Sara. In contrast, these are not the common terrestrial gastropod species that are frequently identified in supra-basal zones of Peoria Loess in the Tunica Hills region of Louisiana and Mississippi (Richards, 1938b; McCraw, 1990; McCraw, pers. comm., 1994). A single representative of two terrestrial gastropods common in Peoria Loess (*Triodopsis albolabris* and *Mesodon* sp.) was retrieved from the exposed bank adjacent to the lower unit excavation borders and one (*?Ventridens ligera*) in the upper unit [although Clark *et al.* (1989) report cf. *Mesodon* sp. characteristic of three samples from Ward Creek]. Numerous calcareous concretions common to loess, what Fisk (1938) refers to as "loess dolls," were found in the lower unit.

Maximum numbers of planorbids are reported to occur in shallow water areas not exceeding 2 meters in depth (Baker, 1945). *Planorbella trivolis* is common in shallow

areas bordered by *Typha* and sedge (Baker, 1945). Algae are a major component of the diet of *Gyraulus parvus*. Leonard (1959) reports that, in Kansas, *G. parvus* is frequently found on or among aquatic plants such as *Chara, Typha, Spirogyra,* and duckweed and on submerged blades of living and dead grasses or on dead tree leaves in water or water-logged driftwood. In New York, Jacobson and Emerson (1961) associate *G. parvus* habitat with the underside of floating wood, lily pads, and rotting leaves and fronds of aquatic plants. Dennis (1928) reported *G. parvus* within a water temperature range of 22°C to 27°C in the Bass Island region of Lake Erie as-

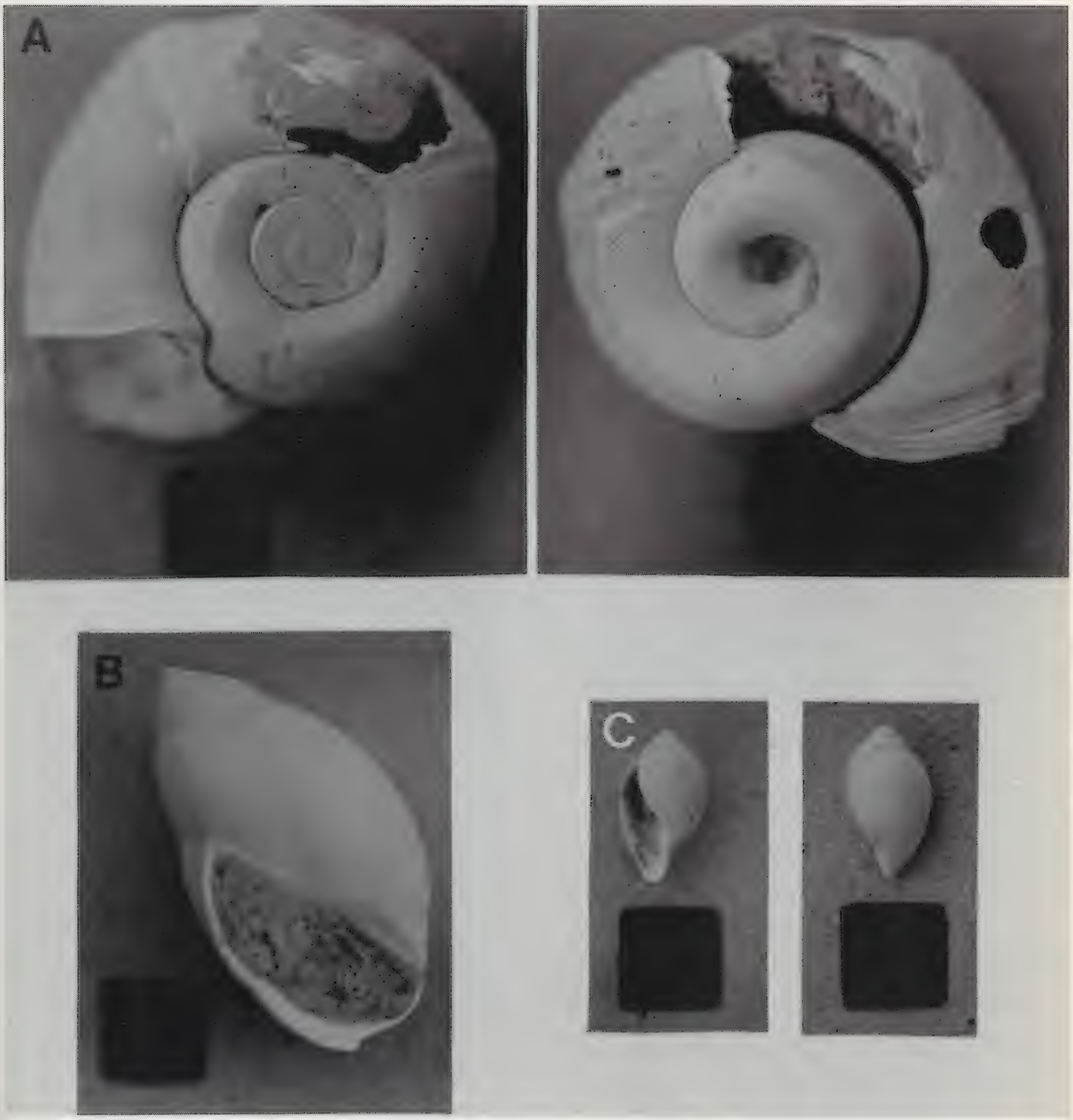


Figure 7. Ward Creek Pleistocene planorbid and physids: (a) apical and umbilical view of *Planorbella trivolis* [x 2.5, WC-91-26a]; (b) sinistral view of *Physella heterostropha* (large form) [x 2.6, WC-91-46]; (c) sinistral and dextral view of *Physella heterostropha* (small form) [x 2.6, WC-91-30b].

sociated with a habitat of abundant vegetation and low velocity, shallow water. Similarly, *Planorbella trivolis* and *Amnicola limosus* are associated with well-vegetated shallow water. The micro-environment at Ward Creek could have been influenced by mastodon bone itself; numerous crevices within cancellous bone structure may have favored algae proliferation. Dominance of *G. parvus* may be a reflection of this altered osseous environment and its associated algal scum. The congregation of these mollusks around the mastodon [as indicated by an inventory of screened sediment samples (Lewis, 1994) and from carbonate fraction (Table 1)] might have facilitated the preservation of mastodon bone by providing an abundant calcium carbonate matrix. This situation could have enhanced the preservation properties of a clay matrix.

Planorbids on the whole can survive in low-oxygen, organic-polluted environments because of their lung-breathing capabilities (Baker, 1945), thus they would not be eliminated from a decaying mammal site. If this was the site of entrapment of this mastodon (for which there is no direct evidence), dominance of planorbids, during a probable Pleistocene decay period for this mastodon, would be a reasonable outcome.

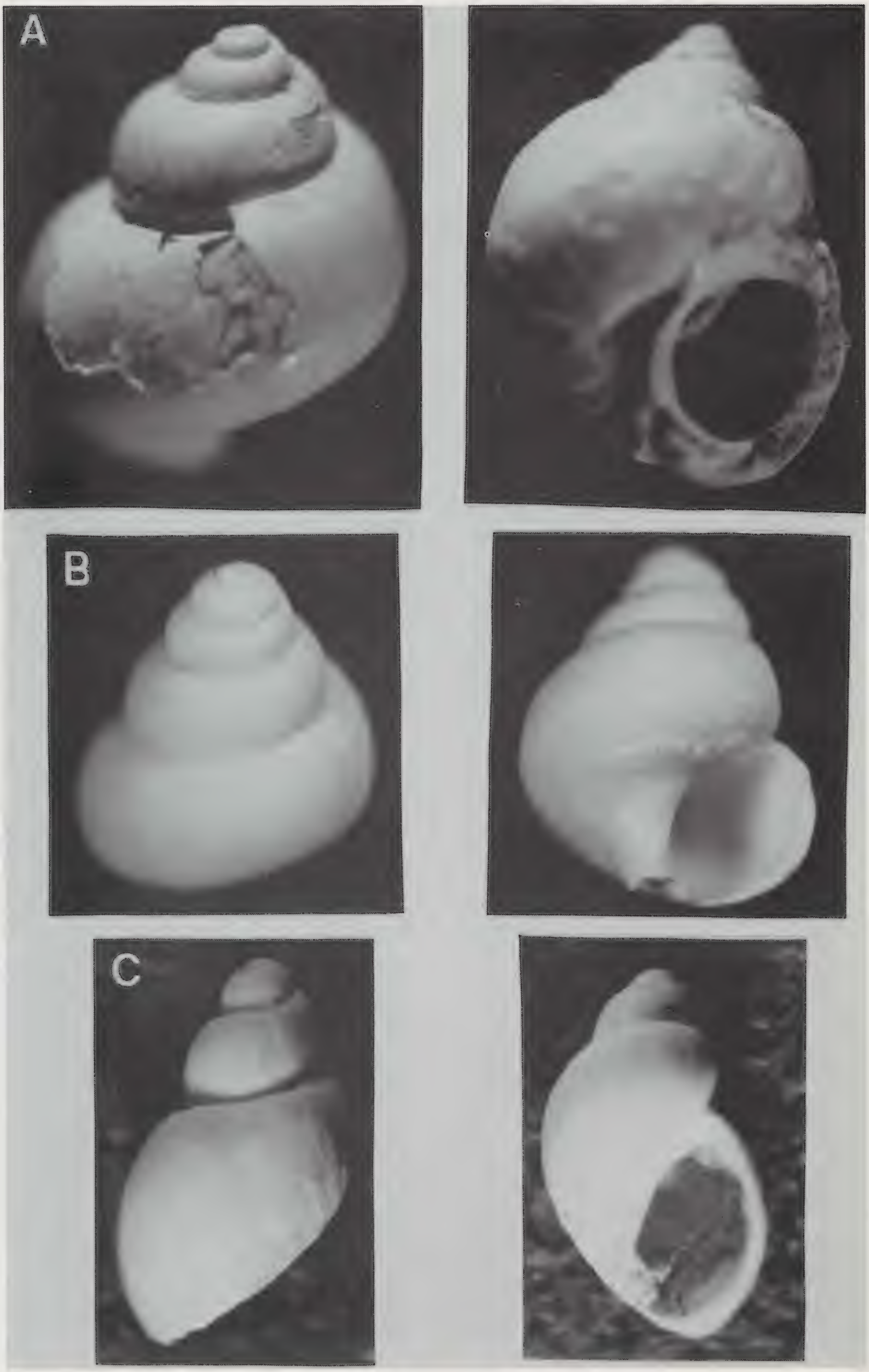
Taxonomic diversity gradients at Ward Creek are informative. The dominance of *Gyraulus parvus* suggests that this gastropod was the superior competitor in this paleoenvironment. Expectations derived from the ecologic postulate of competitive exclusion would be for only a few species to flourish in a given environment and for one species to predominate but not exclude those employing similar feeding methods (Raup and Stanley, 1971). Within this small unit of sediment surrounding the mastodon ulna, *Gyraulus parvus* is the dominant pulmonate feeder of submersed vegetation. *Succinea* sp. and *Pomatiopsis lapidaria* are co-dominate amphibious species. However, *P. lapidaria* inhabits wet ground near water/land interface, whereas *Succinea* sp. clings to vegetation in or near water or inhabits wet leaf mold at the edge of water (Clarke, 1981). *Amnicola limosus* is the dominant non-pulmonate gastropod and is associated with unpolluted, perennial-water habitats where aquatic vegetation grows (Clarke, 1981).

Whether mollusks retrieved from this small excavation unit are representative of a true fossil mollusk community remains an open question. Sampling limitations and differential preservation are factors to be considered. Nonetheless, the dominance of a few species coincides with expectations for a reconstructed fossil microcommunity in this paleoenvironment. It is also to be expected that small numbers of inferior competitors will remain part of the assemblage (Raup and Stanley, 1971). Such appears to be the case at the 1991 Ward Creek excavation site, suggesting that the mollusk assemblage within this microenvironment is indicative of a true fossil community.

As stated previously, the molluscan assemblage from the fossil-yielding unit at Ward Creek is similar to the molluscan assemblage of basal zone Peoria Loess at Percy Bluff along Little Bayou Sara (Richards, 1938a). Peoria Loess in Louisiana is presently assigned earlier inclusive time frames than previously reported (Alford *et al.*, 1983; W. Miller, 1983; B. J. Miller *et al.*, 1985; Clark *et al.*, 1989; B. J. Miller, 1991; Saucier, 1991; Jackson and Givens, 1994). More regionally, an age of 23,900 yr was calculated using electron spin resonance (ESR) dating of mollusk shell from basal Peoria Loess at the Old River section, Tennessee (Skinner and Mirecki, 1993 *in* Mirecki and Miller, 1994). Further north in the Driftless Area, snail shells 25 cm above the base of the Peoria Formation yielded an AMS radiocarbon date of 24,250 $\pm$ 970 ^{14}C yr B.P. (Leigh and Knox, 1994).

Besides evidence from geochronology and mollusk assemblage, sediment characteristics are similar to what B. J. Miller *et al.* (1985) and B. J. Miller *et al.* (1988) refer to as a basal mixed zone of Peoria Loess discernible in the Lower Mississippi Val-

Figure 8. Ward Creek Pleistocene hydrobiid, pyramidellid, and lymnaeid, sinistral and dextral views: (a) *Amnicola limosus* [x 15.0, WC-91-19], (b) ?*Fargoa gibbosa* [x 21.6, WC-91-30c]; (c) *Fossaria parva* [x 23.3, WC-91-6]. >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ley. A body of literature has emerged in recent years documenting a silty clay loam transition zone at basal loess deposits. Basal mixed zones refer to zones exhibiting mixing of loess with underlying material as the result of the processes of bioturbation and pedoturbation (B. J. Miller *et al.*, 1988). Miller (1987) suggests that late phase terrace construction overlapped the early phase of Peoria Loess deposition. Several examples of a mixed zone or transitional silty clay loam, similar in granulometric analysis to screened samples reported here for Ward Creek, are recorded for several sites in Louisiana by B. J. Miller *et al.* (1985). In the Amite River Valley, the oldest Holocene alloformation, the Watson, is underlain by the clay Prairie Terrace (Autin, 1992). Thus, basal zones of the Watson might reflect the apparently ubiquitous presence of loess in the Lower Mississippi Valley during this time period and may be similar to basal Peoria Loess as a result of similar transition zone mixing of silt, silt derived loess, and Prairie Terrace clay. Autin (1993) reports that although the Watson is primarily a Holocene alloformation, the age of initial Watson deposition may be late Wisconsinan when the Amite River was still tributary to an ancestral Florida Parishes drainage basin. At a Ward Creek site Pleistocene swamp, wind blown loess would have been filtered through swamp water, rather than deposited on an exposed surface, the latter being a typical situation for Peoria Loess.

Likewise for the midcontinental United States, McSweeney *et al.* (1988) report of loamy zones containing characteristic pedorelicts which occur as transitional deposits between Wisconsinan loess and underlying soil units. Pedorelicts, such as calcareous nodules and iron oxide nodules, retrieved in screened sediment samples from the fossil yielding clay/silty clay loam at Ward Creek could reasonably be related to *in situ* pedogenic reorganization. This contrasts transition zones of the midcontinental United States where pedorelicts are indicative of disruption, transport, or reorganization of soil (McSweeney *et al.*, 1988).

Bones recovered in 1991 appear to belong to a larger bone assemblage recovered previously at Ward Creek. Although only a mastodon ulna was retrieved at the excavation site on the North Fork of Ward Creek in 1991, previous excavation at this site in 1974 and additional retrieval of bone from 1974 to 1981 yielded a relatively complete adult mastodon skeleton, as well as a limited number of fragments of a juvenile mastodon and isolated elements from additional (two?) adult mastodons. No ulna elements were identified previously. Paleoecology suggests that the Ward Creek mastodons were buried in Pleistocene sediments forming the surface bottom of a shallow water lowland swamp, which was in proximity to upland spruce forests. Studies by Delcourt and Delcourt (1977, 1983) suggest that pine and hardwoods would have been components of this swamp. W. E. Miller (1987) reports that the vast majority of *Mammut americanum* fossils have been recovered from bog, swamp, marsh, or sinkhole situations associated with regions where spruce was abundant. Similarities to the Ward Creek site are discernible in a recent report of a Columbian mammoth (*Mammuthus columbi*) excavated from the Wasatch Mountains of Utah, which indicates that this mammoth became mired in clayey silts of a shallow fossil glacial lake rimmed with sedge and containing spruce macrofossils (Gillette and Madsen, 1993). Interestingly, a high percentage of juvenile or young adult mastodon fossils in these situations suggests that becoming mired in bog-swamp-marsh-sinkhole deposits was a common danger for inexperienced mastodons (W. E. Miller, 1987). For example, a clay-plugged sinkhole resulting from water seepage along a fault line in a spruce/fir region defines the location of juxtaposed fossil sub-adult and mature mastodons excavated from the Wasatch Mountains, Utah (W. E. Miller, 1987). Proximity of the Baton Rouge Fault to the Ward Creek excavation site (Sibley, 1972) poses interesting potential influences and parallels. The Baton Rouge Fault intersects the North Fork of Ward Creek ap-

Figure 9. Ward Creek Pleistocene pomatiopsid and succineid, sinistral and dextral views: (a) *Pomatiopsis lapidaria* [x 16.2, WC-91-30b]; (b) *Succinea ?forsheyi* [x 16.2, WC-91-30b].

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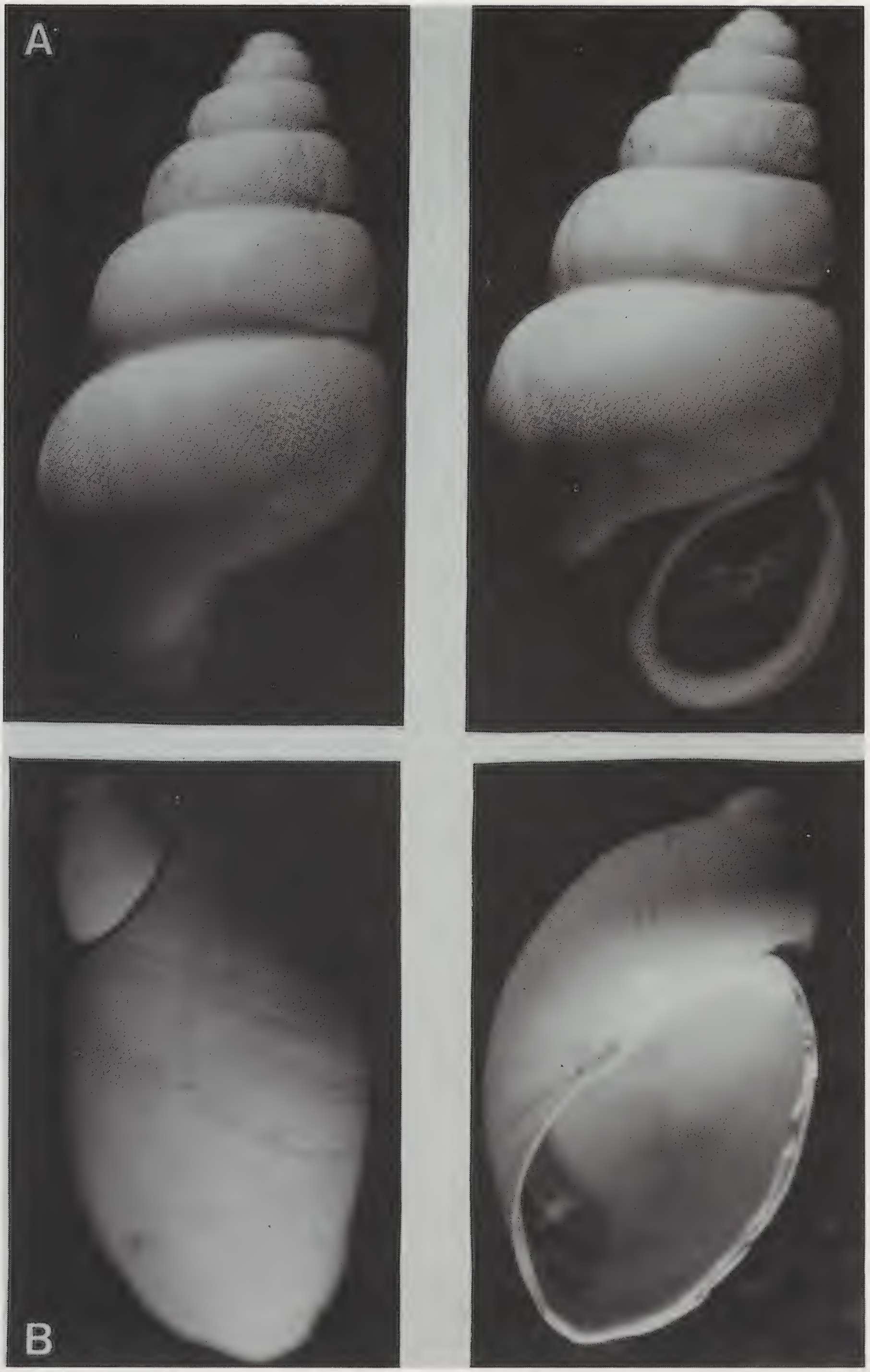
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proximately 0.2 kilometers upstream of the excavation site.

Although the bone is depleted of collagen, the well-preserved cortex retains indicators of muscle attachment sites and vascular or nerve impressions. A few examples of parallel marks consistently spaced 3 mm apart suggest postmortem interaction with this bone by a small mammal. Markings on bone do not resemble those reported as butchering marks from Clovis site mammoths in New Mexico (Saunders *et al.*, 1994) and South Dakota (Hannus, 1990). Although Fisher (1984) reported presence of burned bone at a Paleoindian mastodon site in Michigan, what initially appeared to be charred bone at Ward Creek is better designated postmortem staining of bone.

VI. CONCLUSIONS

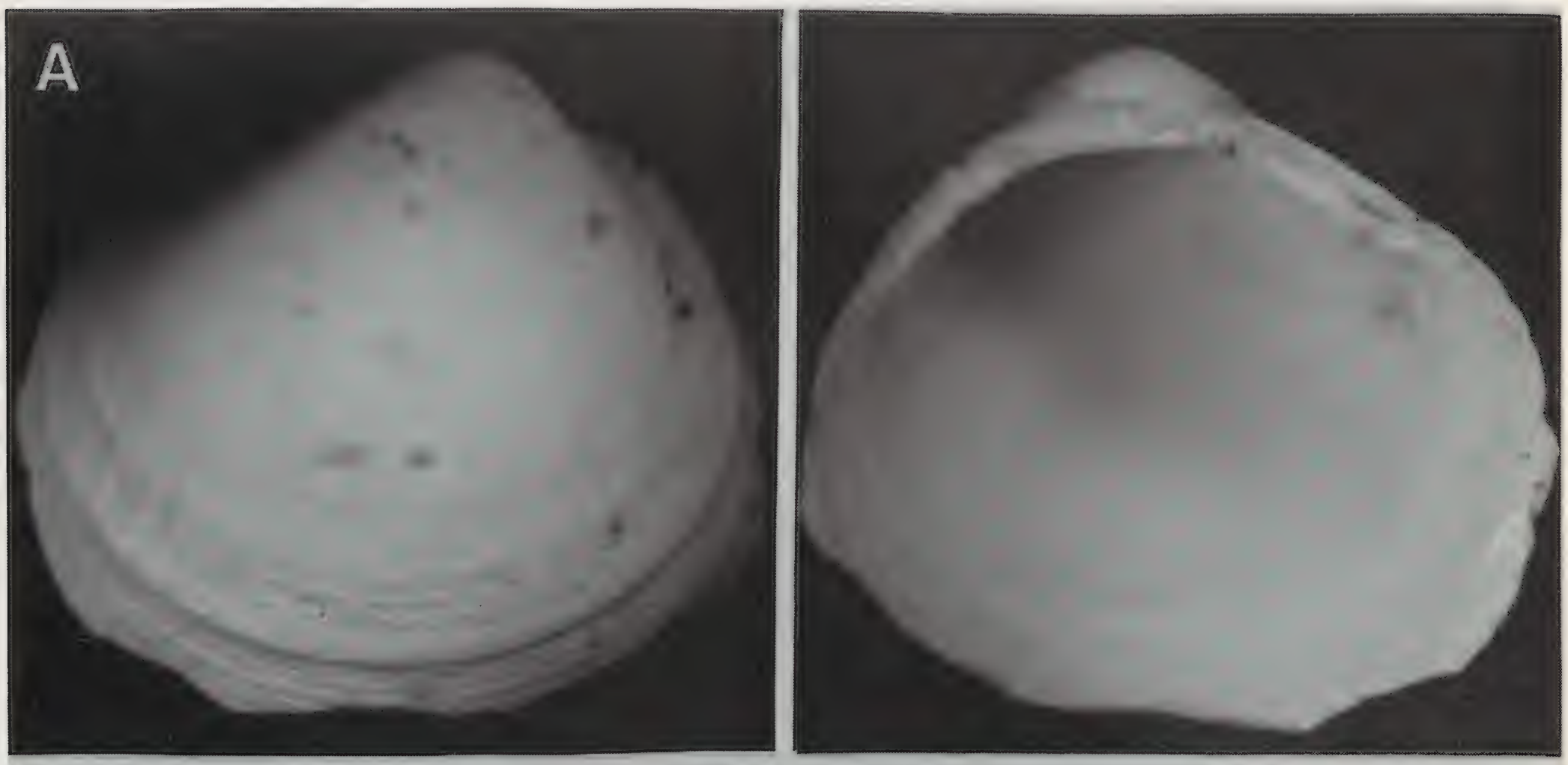
Shell dates, sediment traits, mollusk species, and paleoecology suggest that the excavation unit yielding a fossil mastodon ulna is part of a late Pleistocene swamp subsurface where silt derived from both reworked eolian loess and probable glacial silt deposits combined with terminal Prairie Terrace depositions. This sediment unit is also associated with initial deposition of late Wisconsinan basal loess (sometimes referred to as basal Peoria Loess or pre-Peoria Loess) by correlation with gastropod species (Richards, 1938a), by radiocarbon dates at other sites near the range of 21,220 $\pm$ 360 yr B.P. reported on here (Alford, Kolb, and Holmes, 1983; B. J. Miller *et al.*, 1985; Givens and Givens, 1987; Clark *et al.*, 1989; Autin *et al.*, 1991; Jackson and Givens, 1994), and by sediment characteristics (Richards, 1938a; B. J. Miller *et al.*, 1985; B. J. Miller *et al.*, 1988; McCraw and Autin, 1989; B. J. Miller, 1991). Granulometric analysis suggests this late Wisconsinan sediment to be a clay/silty clay loam. Sediment characteristics and stratigraphy suggest admixture of the Pleistocene Prairie Terrace with initial late Wisconsinan loess at a basal transition zone (B. J. Miller *et al.*, 1985; B. J. Miller *et al.*, 1988). In the Amite River Valley, this transition zone would be between the Pleistocene Prairie Terrace and the overlying Watson alloformation. The fossil yielding unit contrasts more typical and more recent Peoria Loess by mollusk assemblage, radiocarbon date, and sediment characteristics (B. J. Miller *et al.*, 1985; Autin and McCraw, 1989; B. J. Miller, 1991). The fossil mollusk assemblage may be indicative of basal mixed zones in other localities.

The Ward Creek Mastodon ulna was buried in a shallow swamp dominated by Planorbid mollusks. This micro-environment was probably slightly warmer but similar to the synchronous temperate paleoclimate characterized by spruce forests in upland regions of the Tunica Hills north of Ward Creek. Pine and hardwood trees were probable components of this swamp. Influence of climatic factors related to the glacial maximum is inferred.

A few speculations are ventured. Inferred paleoenvironment in conjunction with proximity of this mastodon ulna with previously excavated adult and juvenile mastodon fossil bone from this site on the North Fork of Ward Creek encourages speculation that this was the site of entrapment of these animals. Inferred paleopathology leads the author to speculate that parasitic infection was an environmental stress for mastodons inhabiting a Ward Creek swamp. The dominant mollusk species, *Gyraulus parvus*, as well as several other species retrieved directly from the matrix of this mastodon ulna are known to be intermediate hosts for blood parasites. The density of aquatic mollusk shell around the bone, as determined from inventories of material screened from sediment samples (Lewis, 1994) and carbonate fraction analysis (Table 1), appears to have facilitated preservation of this bone by providing a calcium carbonate matrix.

There is no direct evidence for premortem interaction with this mastodon bone by Paleoindians nor of butchering marks associated with mastodon/mammoth sites

Figure 10. Ward Creek Pleistocene sphaeriid peaclams: (a) left valve *Pisidium ?variabile* [x 17.0, WC-91-41]; (b) left valve *Pisidium ?compressum* [x 15.0, WC-91-19]; (c) right valve *Pisidium ?equilaterale* [x 16.8, WC-91-19]. >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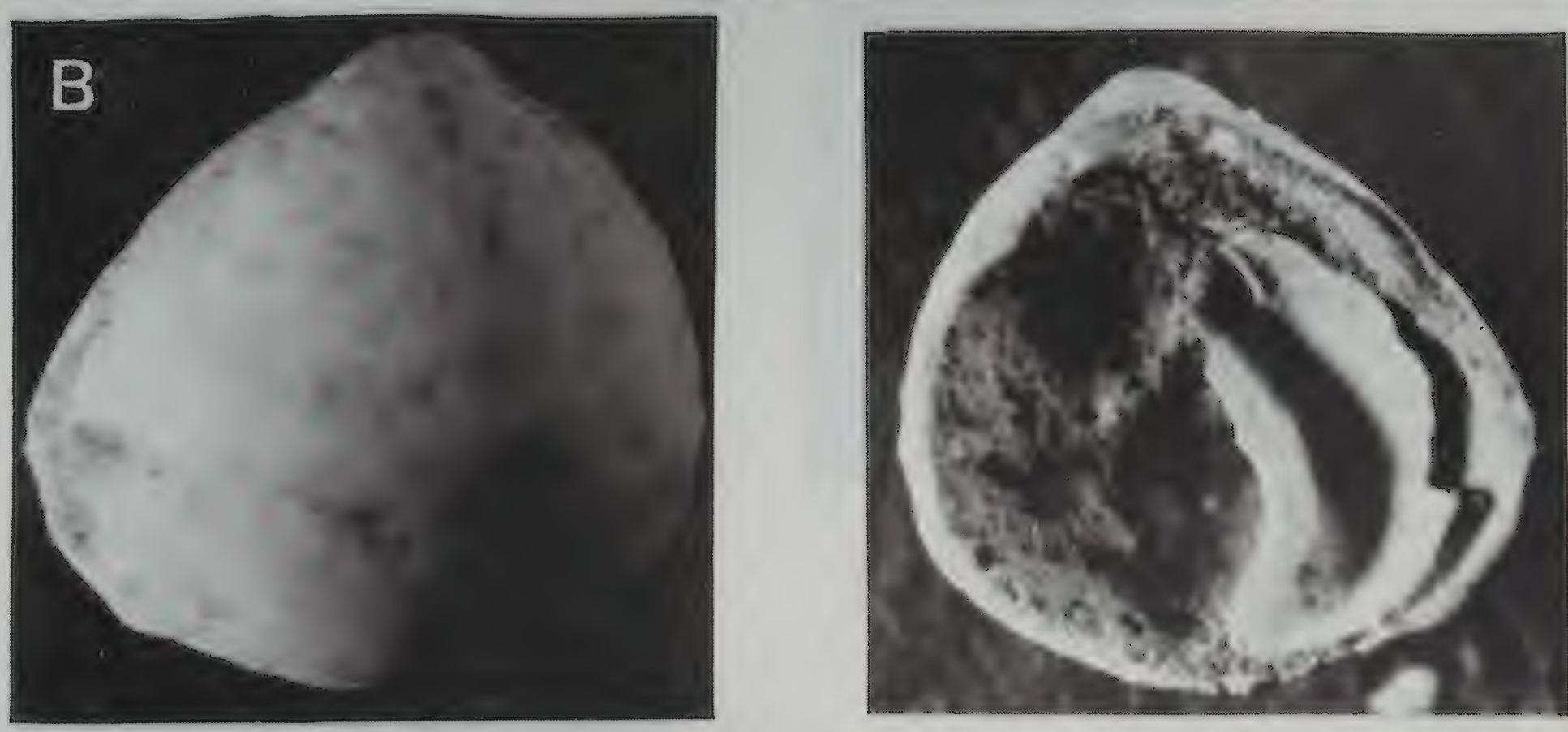
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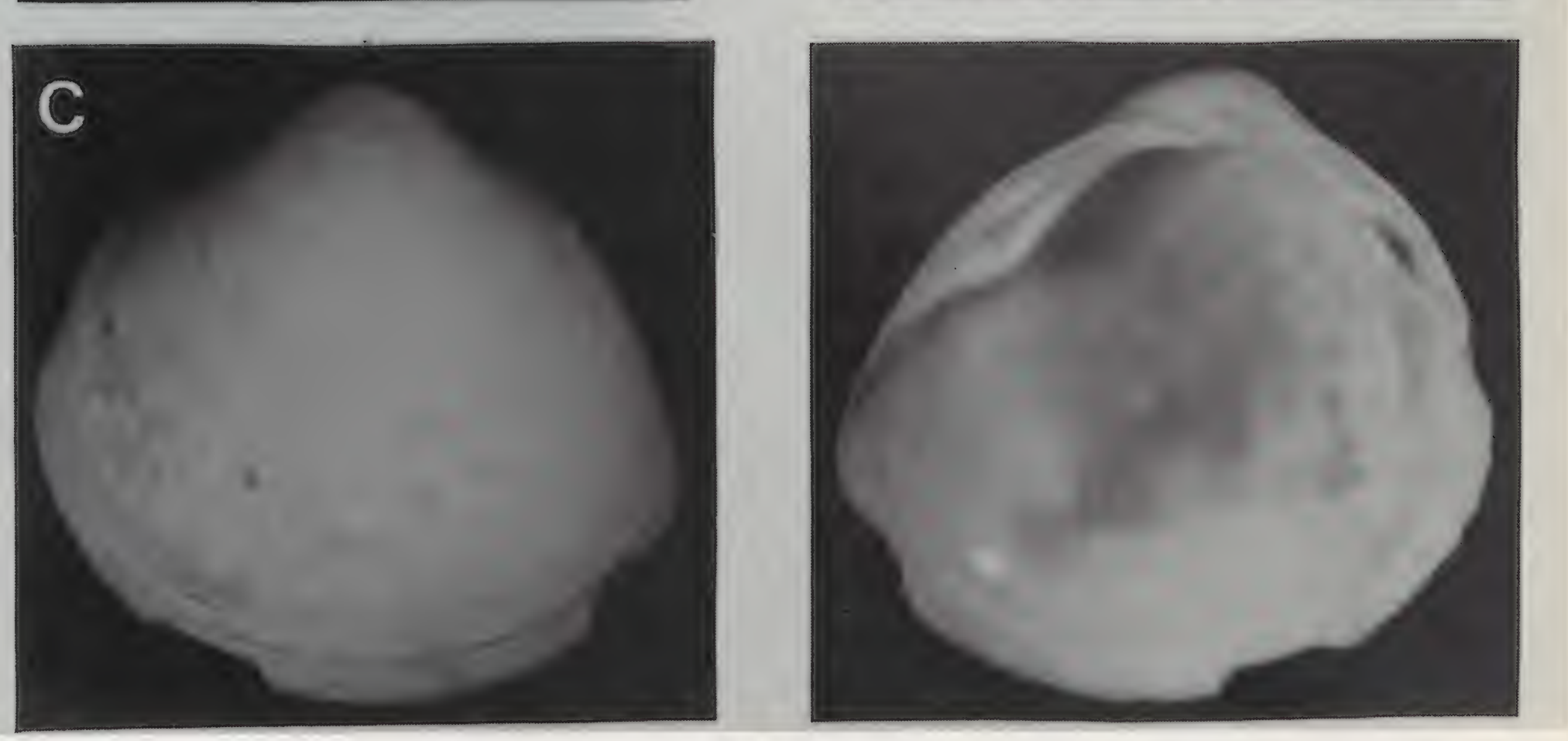
C

elsewhere in North America. There is some evidence for limited postmortem gnawing on the bone by a small mammal. Most markings on the cortex appear to be muscle attachment sites or nerve/vascular impressions.

Frequency of mollusk families within two contrasting excavation units, the bone-bearing Pleistocene unit and the overlying Holocene alluvium/colluvium, is informative. Considering the Class Gastropoda, of the 331 identified individual specimens reported here for the Pleistocene assemblage, planorbids comprise 73% (236/322) of the gastropods present. *Gyraulus parvus* is the most abundant species present, comprising 87% (206/236) of planorbids and 64% (206/322) of gastropods present in the Pleistocene assemblage. Hydrobiids, mainly *Amnicola limosus*, comprise 14% (46/322) of Pleistocene gastropods. Of the 115 specimens identified here for the Holocene unit overlying the fossil-yielding unit, Hydrobiids represent 68% (48/71) and Physids comprise 20% (14/71) of gastropods present in the Holocene assemblage. Planorbids only represent 7% (5/71) of gastropods present in the Holocene assemblage, and this figure may be high due to their suggested intrusive presence in the upper unit. Considering the Class Bivalvia, in the Pleistocene fossil yielding unit, *Pisidium* is the most common bivalve genus, but represents only 2% (7/331) of the Pleistocene mollusks. In contrast, in the Holocene excavation unit, *Sphaerium* and *Musculium* are common.

VII. ACKNOWLEDGMENTS

I thank Dr. John J. Alford for pointing out the research potential at the North Fork of Ward Creek site, for his constructive comments on my interpretations, and for his assistance with the initial excavation at the site along with Joseph Holmes and Dr. Anthony Lewis. Dr. Anthony Lewis of Louisiana State University (LSU) Department of Geography and Anthropology provided ongoing technical and personal support as well as reviews of the manuscript and a site photograph (Fig. 3). Anthropology students of Dr. Heather McKillop, LSU Department of Geography and Anthropology, assisted at the excavation site on 11/1/91. Dr. Lauri Anderson, LSU Department of Geology, provided use of a microscope with a camera. Cindy Henk, LSU Department of Microbiology, assisted with SEM scanning for pollen. Dr. Greg Stone and graduate student Charles K. Armbruster, LSU Department of Geography and Anthropology, provided granulometric analysis of selected samples. Mary Lee Eggart, LSU Department of Geography and Anthropology, prepared the map and site diagram. Dr. Whitney Autin, Louisiana Geological Survey, provided information on regional soils. Bryan Harmon, City of Baton Rouge Drainage Engineer, granted permission for the excavation. Dr. Judith Schiebout and Alvin Phillips of LSU Museum of Natural Science, John Caruso and Michael Taylor of Tulane University Museum of Natural History, Charles Finsley of Dallas Museum of Natural History, Dr. Chris Cunningham of Houston Museum of Natural Science, and Dr. William Orr of the University of Oregon Thomas Condon State Museum of Fossils generously granted access to comparative collections. I thank the reviewers for their helpful comments.

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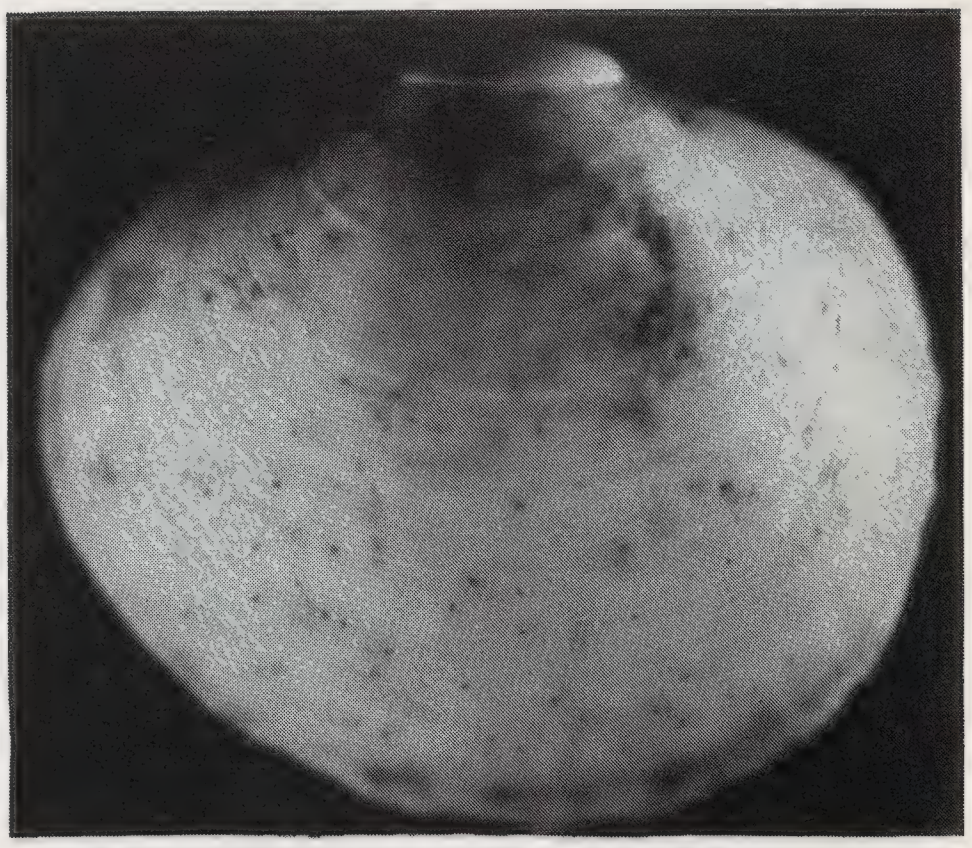

Figure 11. Ward Creek Pleistocene sphaeriid fingernailclam, *Musculium partumeium* [x 12.0, WC-91-20].

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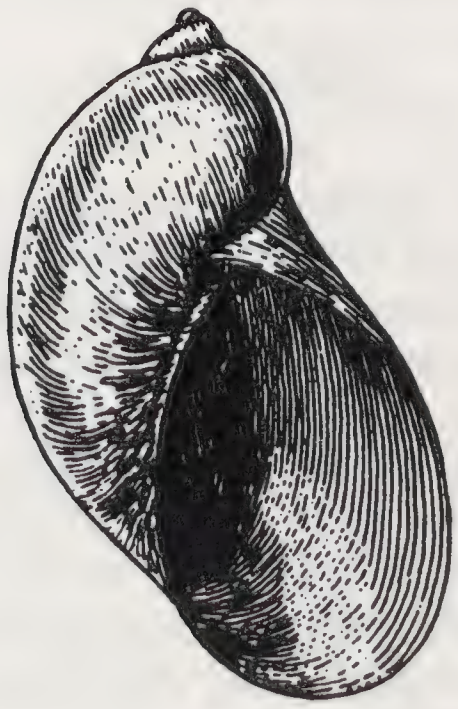

VIGNETTES OF COASTAL PLAIN GEOLOGY

CHARLES LYELL
(1797-1875)

Charles Lyell [after 1848, Sir Charles], accompanied by Lady Lyell, came to the Gulf coastal states on his "*Second Visit to the United States of North America,*" in early 1846. They reached Mobile in mid-February and travelled on the Steamer *James L. Day* through the coastwise "inland passage" to a point where, at daybreak on the 24th, in Lyell's own words,"we found ourselves in Louisiana. We had already entered the large lagoon, called Lake Pontchartrain, by a narrow passage, and, having skirted its southern shore had reached a point six miles north of New Orleans." In a single, short, perceptive, and brilliantly-turned phrase, he both labelled the lake correctly and explained its origin; this remains today a most accurate and clear-cut geological analysis of this lake. From New Orleans, he visited the mouths of the Mississippi River, calculated the age of the lower delta system, described the extended passes of the river, the origin of the "mud lumps," the "fossil forest" in the bluffs at Port Hudson, and collected and described molluscs from the marine Tertiary deposits near Vicksburg; thus, leaving an enduring influence on Gulf Coastal Plain geology.

—H.C.S.

ORIGIN OF MEGAPHYTOCLAST CONCENTRATIONS IN COARSE-GRAINED TURBIDITES, CRETACEOUS OF NORTHERN CALIFORNIA

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ABSTRACT

Coarse-grained, medium- to thick-bedded turbidites in the Franciscan Complex contain carbonized plant debris concentrated in the upper parts of some of the beds. These concentrations typically occur at the top of a thick, graded to massive sand subdivision, and may be covered by a thin, parallel-laminated silt or silty sand subdivision. Plant fragments are usually angular, vary greatly in size and shape, and do not display obvious signs of current orientation. The largest fragments (≥ 1 cm in longest dimension) are here termed *megaphytoclasts*. Accumulations of plant debris in sandy turbidites suggest a complex interaction of water currents with heterogeneous sediment loads in high-concentration turbidity currents.

Phytoclast lamina probably are formed by *hydrofoil stripping*, in which plant fragments are wafted out of sediment gravity flows by currents moving forward and upward through the head regions of the flows, followed immediately by settling of the fragments directly onto newly deposited carpets of turbidite sand. Phytoclast concentrations formed in this way may be buried by fine-grained sediment in the last stage of turbidite emplacement, or plant material may accumulate without further clastic deposition resulting in lamina of deepsea terrigenous coal.

INTRODUCTION

Land-derived plant debris is a familiar component of modern and ancient turbidites (Bouma, 1962; Bouma and Brower, 1964; Griggs *et al.*, 1969; Bostnick, 1974; Bourgeois, 1980; Nilsen, 1984; Nelson and Nilsen, 1984; Bouma *et al.*, 1985; Miller, 1989; Einsele, 1991). In most instances, presence of plant material has been mentioned in descriptions of stratigraphic sections without any further explanation. In a few cases phytoclasts (transported plant material of varied size, shape, and origin) occurring in turbidite sandstone have been used to estimate thermal metamorphic grade (Bostnick, 1974) or to infer paleocurrent direction (Marschalko, 1964). Processes responsible for accumulation of phytoclasts in deepsea depositional environments, however, have never been documented.

Plant fragments also are well known from studies of the modern deep seafloor (see review of early literature in Knudsen, 1961, and Uchupi and Jones, 1967). The significance of plant debris is usually evaluated in ecologic terms: as food resources, special substrata, or as an aspect of disturbance regime (Menzies *et al.*, 1967; Menzies and Rowe, 1969; Keller *et al.*, 1973; Wiebe *et al.*, 1976; Hinga *et al.*, 1979; Rowe and Staresinic; 1979; Wolff, 1976, 1979; Carey, 1981; Stockton and DeLaca, 1982; Grassle and Morse-Porteous, 1987; Alongi, 1990; Gage and Tyler, 1991; Young and Eckelbarger, 1994). Because of the episodic nature of transport and deposition of coarse-grained material in the deep sea, delivery of land-derived plant debris is largely pulsed and linked to events on islands and continents that vary greatly in terms of recurrence interval. Depositional pulses that deliver phytoclasts to off-shelf settings vary from yearly floods at fluvial sources to debris flows originating at the shelf edge, on the slope apron, or within submarine canyons at intervals of $10\text{-}10^3$ yr. In general, the result of such processes is the spatially and temporally discontinuous accumulation of plant fragments. Ultimate sources of large, woody material are forested, emergent landscapes (Gage and Tyler, 1991).

Large plant fragments are mentioned in systematic surveys of components of the deepsea benthos requiring woody substrata (*e.g.*, Knudsen, 1961; Turner, 1973). These large land-derived fragments (referred to here as *megaphytoclasts*, or phytoclasts ≥1 cm in longest dimension) have not been described in studies of ancient deepsea sediments or fossils, so far as I can judge from a review of the literature. Yet the delivery of megaphytoclasts to the deep sea must have been an ongoing pro-

cess at least since the appearance of forests containing large tracheophytes in the Pennsylvanian Period.

In this paper I describe the occurrence of megaphytoclasts in Cretaceous turbidites of the Franciscan Complex in northern coastal California. I will document the sedimentologic contexts of phytoclast concentrations in general, describe a particularly interesting occurrence of unusually large plant fragments, and propose a model to account for megaphytoclast accumulations in sandy turbidites.

STUDY SITES

Coarse-grained, medium- to thick-bedded turbidites were examined during the interval 1984-1988, as part of a larger effort to locate fossil assemblages of all types in different kinds of submarine fan facies of the Franciscan Complex. Three of the sites investigated at that time featured conspicuous phytoclast accumulations, and these localities provided the incentive and material for this study (Fig. 1)

The most carefully studied site (locality 1, Fig. 1) is the seacliff exposure of facies B and C turbidites (traditional facies classification of Mutti and Ricci Lucchi, 1978) at the southern end of Indian Beach, approximately 300 to 400 meters southeast of the village of Trinidad (Trinidad 7.5' quadrangle). At this locality, large bedding-plane exposures could be examined because in some parts of the outcrop beds dip at nearly 90° and strike more or less parallel to the cliffline. This locality is within the Central Melange terrane, as is a second, more remote site (locality 2, Fig. 1) 100 to 200 meters south of the mouth of McNeil Creek (Trinidad 7.5' quadrangle). This also is a seacliff exposure, but consists mostly of facies B deposits. The McNeil Creek site is remarkable because of the occurrence of soft-coal laminae at the tops of a few of the thick-bedded turbidites in lieu of the typical pelitic layers. The third site (locality 3, Fig. 1) is within the Yolla Bolly terrane at Point Saint George (Crescent City 7.5' quadrangle), and comprises a quarried cliffline and headland extending from 250 meters west to 450 meters south of the old Coast Guard Station. Facies A and B turbidites occur in these exposures. All turbidite beds examined were Cretaceous in age.

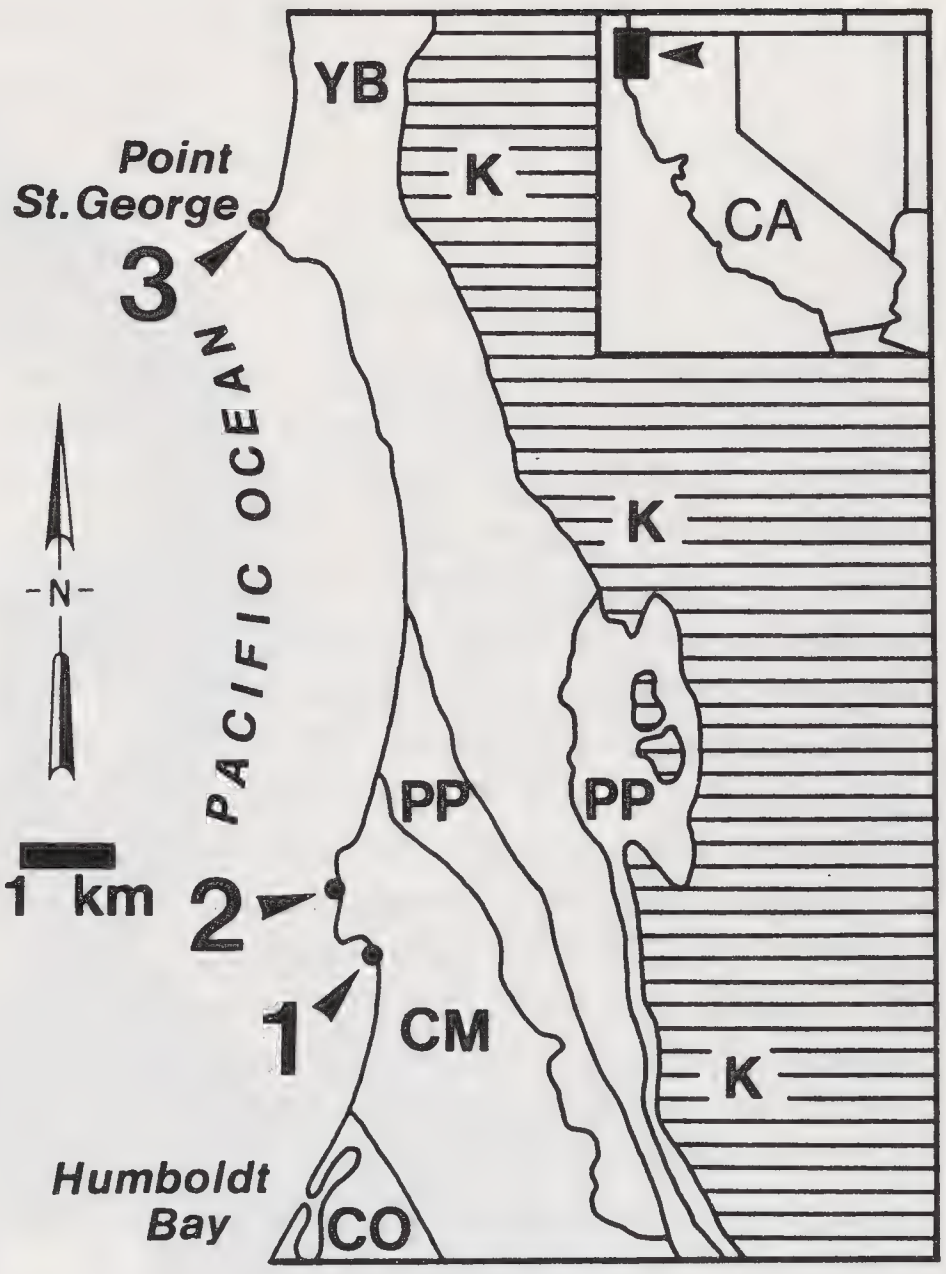

Figure 1. Location of study sites. Tectono-stratigraphic terranes include: *K*, Klamath Province undifferentiated; *PP*, Pickett Peak; *YB*, Yolla Bolly; *CM*, Central Melange; *CO*, Coastal. All but the first are within the Franciscan Complex. (After Aalto, 1989.) Sites are described in the text.

Structure and stratigraphy of Franciscan rocks in the vicinity of localities 1 and 2 have been described by Aalto (1976); the Franciscan geology at locality 3 has been documented by Aalto and Murphy (1984). Terrane terminology and sequence ages are reviewed in Aalto (1989) and Miller (1991, 1993), respectively.

STRATAL PATTERNS

At the three study sites, phytoclast accumulations are restricted to the upper portions or tops of sandy turbidites. This recurrent pattern is a conspicuous feature at outcrops because the turbidite beds fracture readily parallel to bedding at the level of plant debris, revealing surfaces covered with dark-colored, carbonized fragments of varied size and shape (Fig. 2). Where bedding is perpendicular to the out-

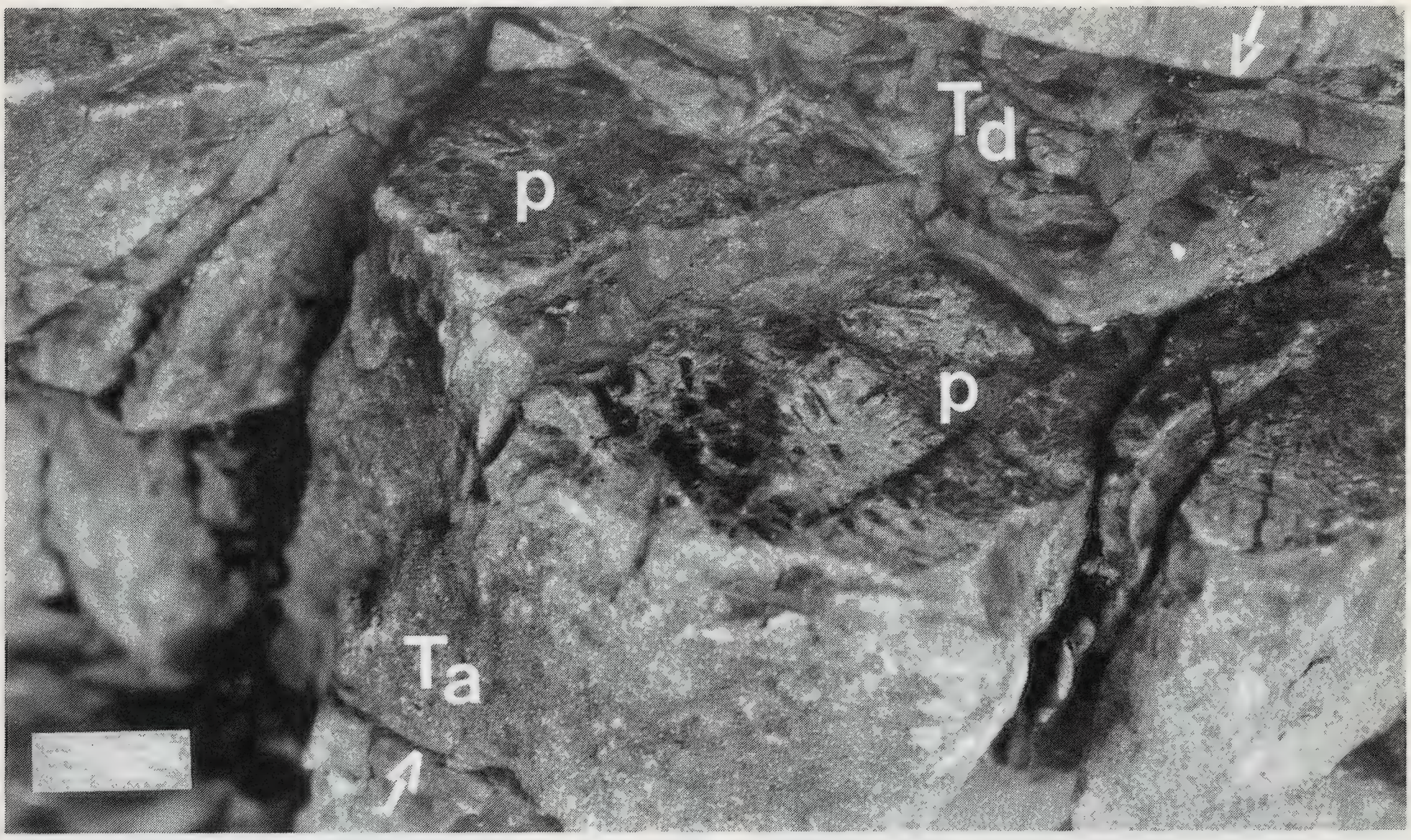

Figure 2. Typical phytoclast concentration (*p*) in Facies C turbidite bed at Indian Beach (locality 1, Fig. 1). Top and bottom of bed are indicated with arrows. Plant debris is concentrated at boundary between Bouma a and d subdivisions. Scale represents 5 cm.

crop surface, a thin, discontinuous black streak (weathering yellowish gray to light brown) denotes the phytoclast layer (Fig. 3a). Plant debris mostly consists of angular, mm- to cm-sized fragments showing no obvious preferred orientation (Fig. 3b), but larger phytoclasts and rounded fragments also were observed (Fig. 3c and e). By comparison, thin sections of sand subdivisions of turbidites from the Central Melange and Yolla Bolly terranes contain microscopic plant material distributed with mineral grains; and there is evidence from trace fossils produced by the benthos, which colonized newly-deposited turbidite sands, that these smaller particles were exploited as food (Miller, 1991). Patterns noted at the three study sites are described in more detail below.

Locality 1. – Facies C turbidites at Indian Beach (Fig. 1) feature a thick, lower, usually normally-graded subdivision overlain by one or more parallel-laminated silt or silty-sand subdivisions. In all beds containing phytoclast layers, the plant debris was concentrated between these two stratal divisions; or in the case of repeated silty units, at the base of each silty subdivision (Figs. 2, 3a, 4c and d). The pattern is indicative of some form of sorting and concentration of plant debris.

The largest megaphytoclasts were found at Indian Beach, apparently concentrated at tops of facies B deposits. The largest fragment observed was a rectangular piece, measuring approximately 23 x 22 cm, which appears to be a trunk or limb fragment displaying subparallel lineation that could be remnant fibrous tissue (Fig. 3c). Stem-like fragments up to 20 cm in length are more typical (Fig. 3e). The megaphytoclasts occur in layers consisting mostly of smaller debris.

Locality 2. – Most of the deposits at McNeil Creek (Fig. 1) are thick-bedded facies B turbidites. The same general stratal patterns were seen here, with the notable exception of coaly layers located at tops of some of the beds (Fig. 3f, 4b). Coal laminae are only a few mm thick and form flat lenses. The laminae apparently represent concentrations of plant debris to the exclusion of mineral clasts following emplacement of coarse, thick turbidite

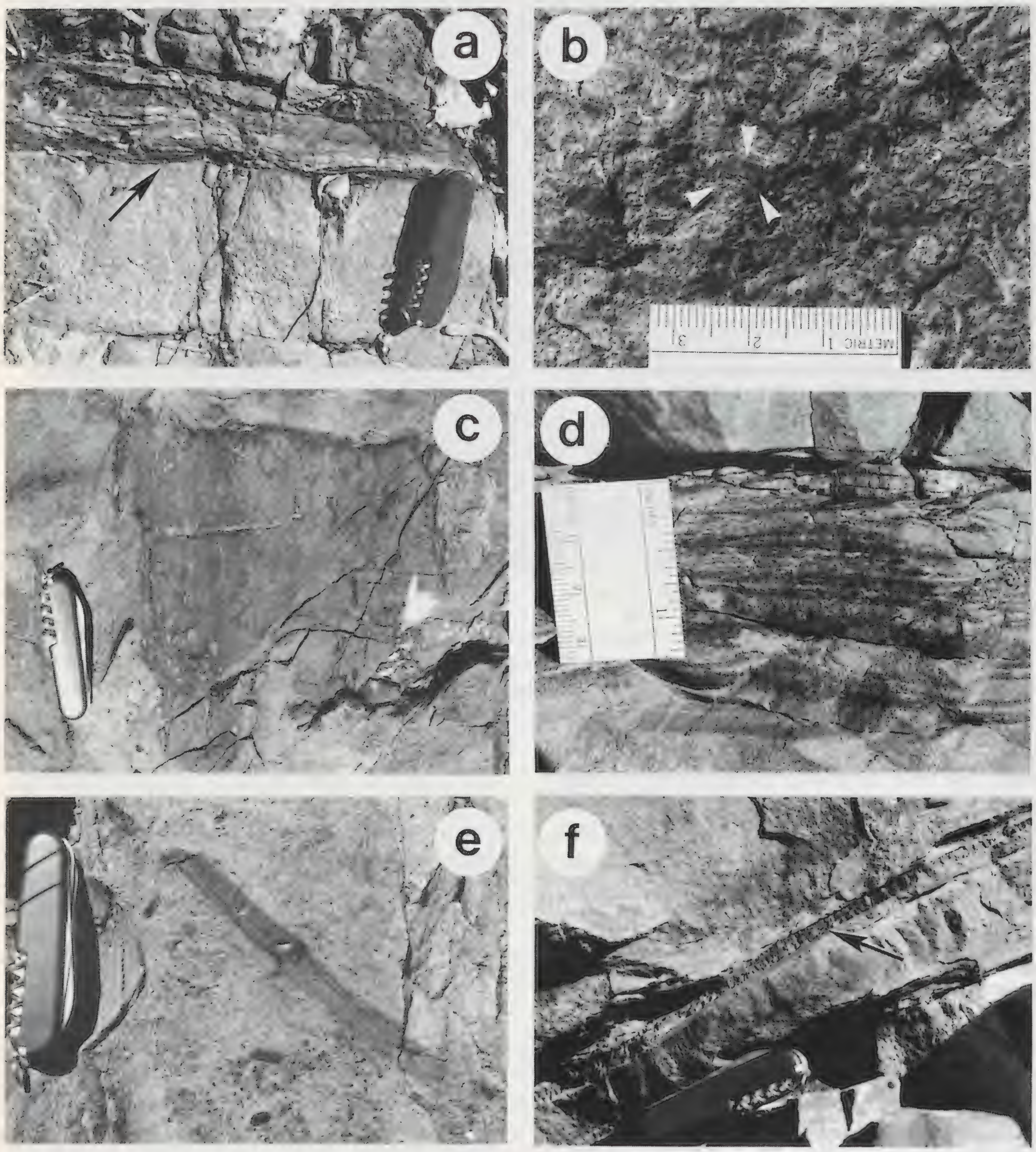

Figure 3. Examples of phytoclast concentrations: *a*, plant debris layer (arrow) at boundary between Bouma a and d subdivisions, Indian Beach near Trinidad (locality 1, Fig. 1); *b*, fracture surface covered with carbonized plant fragments, Indian Beach; *c*, large rectangular phytoclast, Indian Beach; *d*, repeated phytolast laminae at the top of thick sand subdivision, Point Saint George (locality 3); *e*, stem-like megaphytoclast, Indian Beach; *f*, soft coal lamina (arrow), near McNeil Creek (locality 2). Knife in a, c, e and f is 9 cm long.

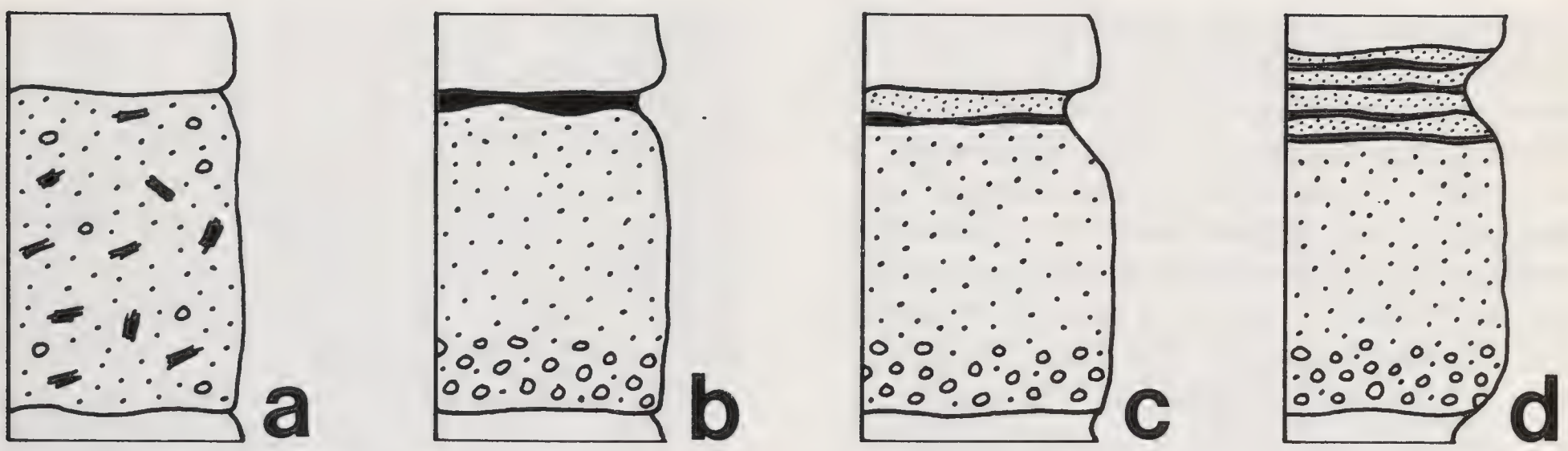

Figure 4. Occurrence of phytoclasts in Franciscan turbidites: *a*, distributed throughout bed (typically as microscopic particles); *b*, coaly lamina at top of thick, coarse-grained subdivision; *c*, concentration between coarse sand and silty subdivisions near top of bed; *d*, multiple concentrations near top of bed. Not drawn to scale.

sand layers. To my knowledge, this is the first record of *deepsea terrigenous coal.*

Locality 3. – Because the seacliffs and headlands at Point Saint George (Fig. 1) were quarried to repair the harbor at Crescent City following the 1964 tsunamis, good exposures of facies A and B turbidites can be seen at this site. Phytoclasts occur as scattered dark grains in a few of the conglomeratic facies A beds (Fig. 4a). Where plant debris occurs in the facies B deposits, it is usually concentrated at bases of repeated sandy laminae/thin beds located at tops of the thick massive to graded sandstones (Fig. 3d). This material consists of mm-sized plant fragments. Megaphytoclasts were uncommon in these beds. Size differences in plant debris between otherwise similar turbidite beds, as between here and Indian Beach, could have more to do with the characteristics of supply of plant fragments than with hydraulic processes at ths site of deposition.

ORIGIN OF PLANT DEBRIS CONCENTRATIONS IN FRANCISCAN TURBIDITES

An explanation for the origin of megaphytoclast or coaly layers in sandy turbidites must account for the following patterns:

1) Concentrations occur in facies B and C turbidites.

2) Coarse plant debris is concentrated in one or more laminae/thin beds at tops of graded to massive sand divisions of the turbidite beds.

3) Only microscopic plant material occurs *within* the thick sand divisions.

4) In facies B and C, large plant fragments tend to be concentrated at the boundary between Bouma a and d subdivisions.

5) Within the phytoclast concentrations, size sorting is poor, and the plant fragments are mostly angular and range from mm-sized to 10's-of-cm's in longest dimension.

6) Plant fragments have varied shapes and typically are not current oriented.

Most turbidite sandstones represent essentially single surges of turbulent flow originating from single point-sources or source zones on adjacent slopes or within submarine canyons (Middleton and Hampton, 1976; Nelson and Nilsen, 1984; Einsele, 1991). Merely invoking differential settling velocities to explain sorting and concentration of large phytoclasts is too simplistic. It fails to consider interaction of hydraulic processes of high-concentration turbidity currents with the complex mixture of sediments carried in the flow, including plant material of varied size and shape. Concentration must involve removal of the plant material from the turbidity current before deposition of the heaviest mineral grains. Such plant debris layers mark a level of change in the local hydraulic environment as the turbidity current passes over a patch of seafloor.

I propose that the megaphytoclast layers result from *hydrofoil stripping* of plant material in the turbulent head region of turbidity currents. Behavior of subaqueous

gravity flows has been studied extensively in flume models and to a lesser degree in modern environments (reviewed in Middleton and Hampton, 1976; Pickering *et al.*, 1989). Plant debris, consisting of rectangular, disc-shaped and flat cylindrical fragments, are probably wafted out of the gravity flow by currents moving forward and upward through the head (Fig. 5a). After rapid deposition of the coarsest mineral component, plant fragments stripped from the turbidity current fall immediately from turbulent suspension onto the newly deposited sand blanket (Fig. 5b), followed by accumulation of fine-grained mineral clasts either deposited from suspension or entrained by the remnant boundary currents (Fig. 5c). Separation of grains, then, represents an internal sorting process that depends on: 1) physical properties of plant fragments (*i.e.*, shape and possibly size) that permit wafting; 2) the pattern of water currents within the head and neck areas of flows; and 3) the fact that sediment within the flow initially was a heterogeneous mixture of sand (and possibly granules), mud and plant debris.

The basic stratal pattern resulting from hydrofoil stripping is shown in Figure 4c. Variations include the coal laminae seen at McNeil Creek, which seem to result from the same process in the absence of fine-grained mineral clasts capping the bed (Fig. 4b). Cyclic phytoclast layers at tops of turbidites (Fig. 4d) could represent repeated resuspension and settling of plant debris after the main body of the turbidity current has passed, possibly caused by boundary layer currents (Middleton and Hampton, 1976, p. 201). Discontinuous distribution of megaphytoclasts in a particular sequence of beds could be related either to variation in plant-debris content of individual flows or to the possibility that hydrofoil stripping occurs intermittently as current patterns vary in the head region of turbidity currents. Such hydraulic properties are expected to change with varying sediment concentration and slope of the seafloor, that is with density and velocity.

SIGNIFICANCE

The obvious point to make here is that megaphytoclast concentrations indicate the complexity of water current-sediment particle interactions within turbidity currents. The process of hydrofoil stripping, as it seems to be reflected in the Franciscan turbidite sandstones, only operates in relatively high-density turbidity flows containing plant fragments together with abundant sand and mud. The plant debris can be concentrated only when currents circulating through the head of the flow are able to strip out this material, which is permitted by physical properties of the plant fragments such as shape. These ideas need to be tested in flume experiments.

From a paleontologic perspective, there are two important implications that deserve further study. First, if identifiable

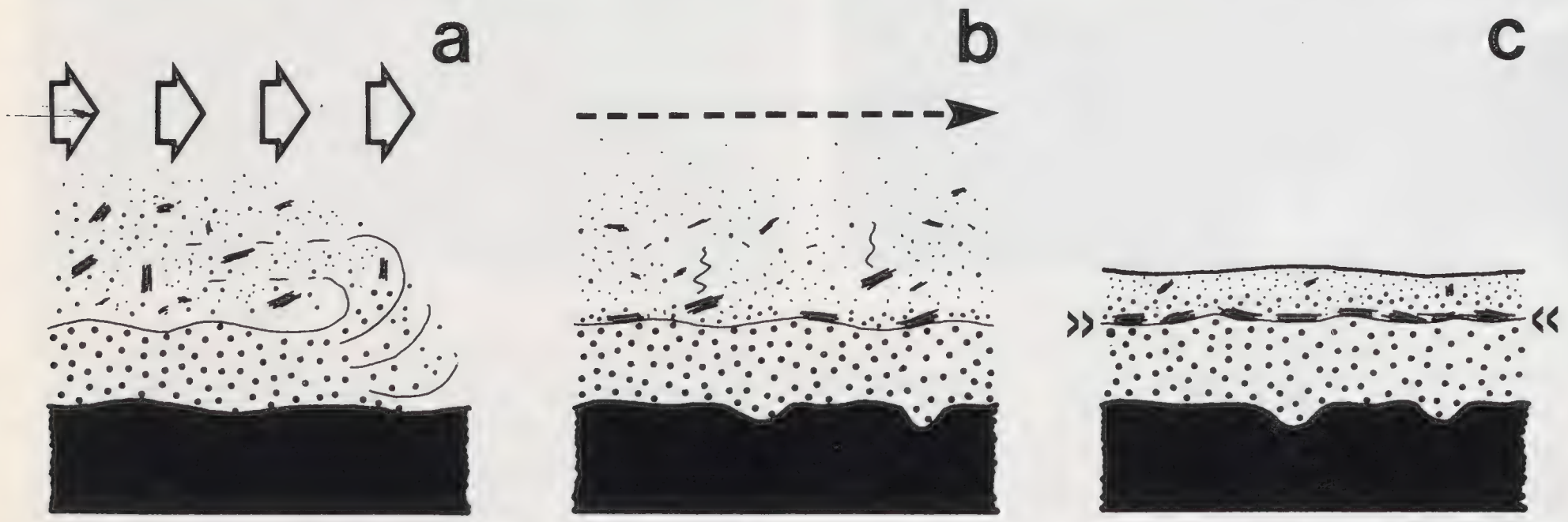

Figure 5. Concentration of megaphytoclasts by means of *hydrofoil stripping: a*, separation of plant debris by currents circulating through head region of turbidity current; *b*, immediate fall out from suspension onto surface of newly deposited turbidite sand; *c*, burial of plant debris beneath silt/silty sand from suspension or entrained in boundary current, completing deposition of the turbidite bed.

land-derived plants (organs, identifiable tissue) occur in the megaphytoclast or coaly laminae of turbidites, paleoclimatic conditions could be deduced for adjacent terrestrial areas. No identifiable specimens were recovered from the Franciscan beds, however, but concentrated searching might yield such material (especially in areas where metamorphic alteration of sandstones has not occurred). Second, deepsea benthos must have utilized or manipulated the windfall of organic material, even though rapid burial presumably would have prevented exploitation by epibenthos such as wood-boring clams. Megaphytoclast concentrations in Franciscan turbidites appear to be undisturbed by burrowers. Perhaps such layers are difficult to penetrate by endobenthic animals, or plant material was too coarse to digest even if laced with labile bacteria and fungi (Wolff, 1979; Gage and Tyler, 1991). Here again, concentrated prospecting might produce evidence of plant debris utilization by burrowing organisms that colonized newly deposited turbidite sand blankets.

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HOLOCENE *ASTRANGIA* (SCLERACTINIA) IN FORESHORE SHELL ACCUMULATIONS, BOGUE BANKS, NORTH CAROLINA

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ABSTRACT

Shell accumulations in the foreshore zone at Pine Knoll Shores, near the eastern end of Bogue Banks, contain a complex environmental and temporal mixture of molluscs, including Pleistocene estuarine species, subfossil marine Holocene material, and modern shells derived mostly from the adjacent shoreface. Mixed with these shells are the coralla of *Astrangia danae*, also mostly derived from the modern shoreface. The coral colonized mollusc shells from a variety of sources during varied intervals of exposure at the seafloor. Occurrence of the coral facilitates identification of pathways of shell transport and shell exposure intervals in modern nearshore environments. *Astrangia danae* is interesting in its own right because it is one of the only shallow-water scleractinians now living in the Cape Lookout area.

INTRODUCTION

Shell accumulations on the ocean beach of Bogue Banks, located at the southern terminus of the North Carolina Outer Banks, consist of complex mixtures of Holocene, Pleistocene, and occasionally older skeletal remains. Fragments and whole valves of gastropod and bivalve molluscs make up the bulk of these localized concentrations. At some locations scleractinian coralla, either attached to molluscs or occurring as unattached bioclasts, can be found in the shell accumulations.

In the latitude of Cape Lookout, scleractinians make their last strong showing in the faunal inventories of late Pliocene-early Pleistocene formations (Tuomey and Holmes, 1857; Vaughan, 1904; DuBar, Solliday, and Howard, 1974; DuBar, Johnson, Thom, and Hatchell, 1974; Bailey and Tedesco, 1986; Carter *et al.*, 1988). By comparison, only *Astrangia* is usually listed as a minor component of the shallow marine fauna from younger units (Clark, 1906; Richards, 1950; DuBar, Solliday, and Howard, 1974; Spencer and Campbell, 1987). *Astrangia* and *Oculina* appear to be the only scleractinians still living in modern shallow marine environments of the region (Verrill, 1872; McDougall, 1943; Field, 1949; Stephenson and Stephenson, 1952; Wass, 1963; Gosner, 1971, 1978). A slightly richer coral assemblage occurs today in offshore Onslow Bay, at depths of 20-30 meters on rock outcrops (MacIntyre and Pilkey, 1969). Other than entries in species lists, often with little explanation or additional data, *Astrangia* has not been studied in nearshore settings of the central coast of North Carolina.

In this report, I describe *Astrangia* coralla from shell accumulations sampled at Pine Knoll Shores (Fig. 1), approximately 13-17 km west of Beaufort Inlet. Specimens were collected by simply picking through the shelly concentrations during low tides in the early summers of 1992-1994. Because there is confusion in the literature concerning species determinations, I will evaluate taxonomic status of the corals from Pine Knoll Shores. The corals encrust modern, subfossil and Pleistocene mollusc shells at this collecting site, and it appears that they can be used as "taphonomic tracers" to map generalized redistribution pathways of shells moving through coastal depositional environments. All specimens used in this study are stored in the Geology Department collection, Humboldt State University.

GEOLOGIC AND ENVIRONMENTAL CONTEXTS

Shell accumulations at Pine Knoll Shores cover areas in the order of 1- 10 m^2, and are spaced at intervals of 10's- to 100's-of-meters in the foreshore zone. The accumulations are ephemeral in the sense that tidal cycles result in periodic reworking of shells and relocation of shelly patches on a time scale of days to months. Shells and other skeletal material include freshly killed specimens that may have soft tissues still attached, "brown shells" from Holocene and Pleistocene sources, and "black shells" of mostly estuarine molluscs reworked from Pleistocene outcrops at the seafloor (see Pilkey *et al.*, 1969). Preservation of individual mollusc specimens ranged from pristine articulated shells and disarticulated valves to unidentifiable

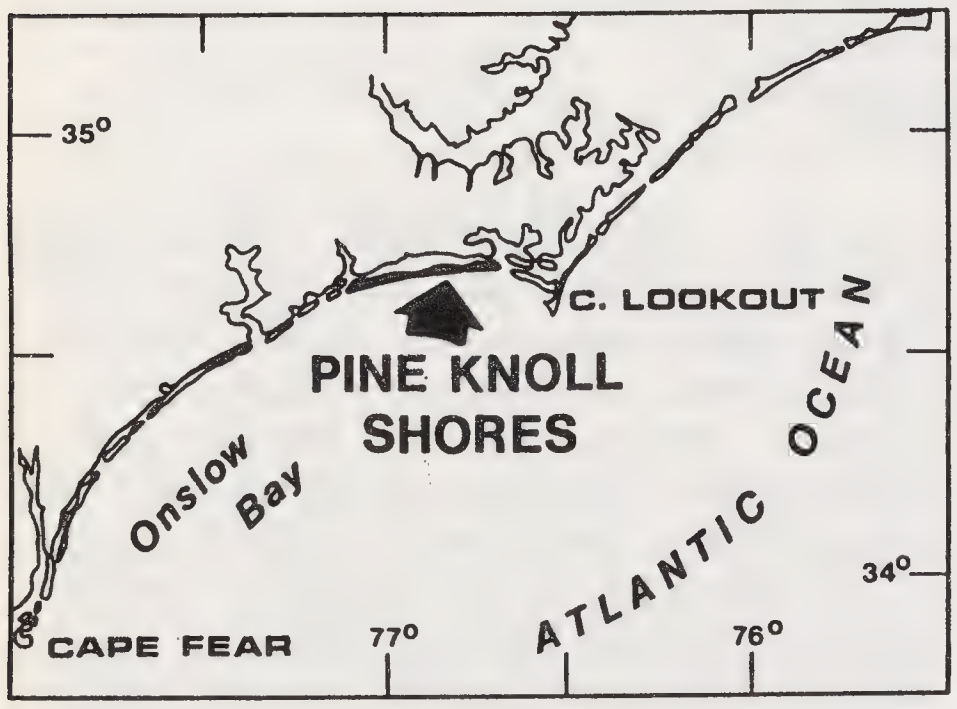

Figure 1. Map showing location of collecting site on Bogue Banks.

scraps. There were no clear trends in source or preservation quality of shells along the approximately 4 km stretch of beach examined. All *Astrangia* specimens appear to be recently killed or subfossil Holocene material.

Bogue Banks is a wave-dominated, microtidal barrier island having well-developed, multiple dune ridges and few washover fans. The island is oriented east-west, unlike most of the barrier segments of the Outer Banks, and encloses a narrow, shallow lagoon (Cleary and Hosier, 1979). Although cottages and hotels cover much of the dune topography, jetties and other sand-conserving structures are mostly absent from the ocean beach. Sand replenishment of the beach appears to be derived from the nearshore zone. An attempt was made in this study to avoid shell accumulations reworked from these replenishment deposits. "Natural" foreshore deposits at Pine Knoll Shores consist of very light tan, fine to coarse, mostly well-sorted, quartz sand containing shell fragments.

Pleistocene-Holocene stratigraphy of Bogue Banks has been described by Moslow and Heron (1986). They recorded 15-20 meters of dune/overwash and foreshore/shoreface sands overlying discontinuous pockets of inlet and backbarrier deposits that were ‹ 5 meters thick, all of Holocene age. The Pleistocene basement occurs at depths from roughly 10 to 20 meters below mean sea level. The Pleistocene units represent a variety of nearshore marine and estuarine facies comparable to modern depositional environments in the area (Mixon and Pilkey, 1976), and their seaward equivalents appear to be the sources for some of the oldest shells at Pine Knoll Shores. Relict Holocene deposits also contribute shells to the beach.

TAXONOMIC STATUS

Astrangia specimens collected from the Beaufort area have been referred to both *A. danae* (*e.g.*, McDougall, 1943; Field, 1949) and to *A. astraeiformis* (*e.g.*, Stephenson and Stephenson, 1952; MacIntyre and Pilkey, 1969)*. The chief differences between these species seem to be (1) corallite packing (the former is plocoid, the latter cerioid) and (2) geographic distribution (*A. danae* is usually regarded as a Virginian Province species; *A. astraeiformis* is supposed to belong to the Carolinian Province). A cerioid corallum collected south of Cape Hatteras, according to these criteria, should be referred to *A. astraeiformis*. Viewed in this way the western Atlantic *Astrangia* comprise a morphocline in corallum organization, possibly related to the inter-regional thermal gradient.

On the other hand, Verrill (1872, p. 436-437) noted that the two species may occur together in the same collecting area, with the plocoid form being more common at higher (cooler) latitudes (see Gosner, 1971, 1978). Verrill regarded *A. astraeiformis* as a junior synonym of *A. danae*. Interestingly, Richards (1950, fig. 75k) illustrated a

*The correct author and date for these two species is subject to some confusion. Certain workers cite *Astrangia danae* as of Agassiz, 1847, but I have been unable to locate this reference. According to Sherborn (*Index Animalium*), Agassiz did not describe *A. danae* until 1850 (Proc. Amer. Assoc. Advanc. Sci., v. 2, p. 69), wherein he states "I propose to dedicate the species to the able describer and illustrator ... and call it in future *Astrangia Danae*." However, also according to Sherborn, in 1849 (Ann. Sci. Nat., [3] Zool., p. xii; Sept., 1849 *fide* Sherborn) Milne-Edwards and Haime described both *A. danae* (p. 180) and *A. astraeiformis* (p. 181). Unless the Agassiz, 1847, reference can be discovered, *A. danae* Milne-Edwards and Haime, 1849, is the older name and would have one page priority over *A. astraeiformis*, if the two species prove to be synonymous.

specimen identified as *A. danae*, from Pleistocene deposits in Hyde County, North Carolina, that featured both plocoid and cerioid organization *in the same corallum*. Biologic properties of *A. danae* have been described in detail by Field (1949) and Waterman (1950).

Specimens from Pine Knoll Shores are intermediate between typical *A. danae* and *astraeiformis*. I will follow Verrill (1872) and use *A. danae* as the appropriate species name, and consider the grades of corallite packing to be morphs. Some specimens were clearly cerioid (Fig. 3A), but others have raised corallites that could be described as subplocoid (Fig. 3B). In all cases, septa are dentate and axial parts of unabraded corallites feature a distinctly papillary columella (see Wells, 1956, p. F408-F409). The intermediate morph from Pine Knoll Shores might represent the geographic transition between dominantly plocoid forms of the Virginian Province and the dominantly cerioid forms of the Carolinian Province. Alternatively, plocoid and cerioid morphs could occur in the same area, and possibly reflect corallum response to short-term climate cycles or fluctuation in other environmental factors. These possibilities need to be tested through a comprehensive autecologic evaluation of *A. danae* from different localities within both provinces.

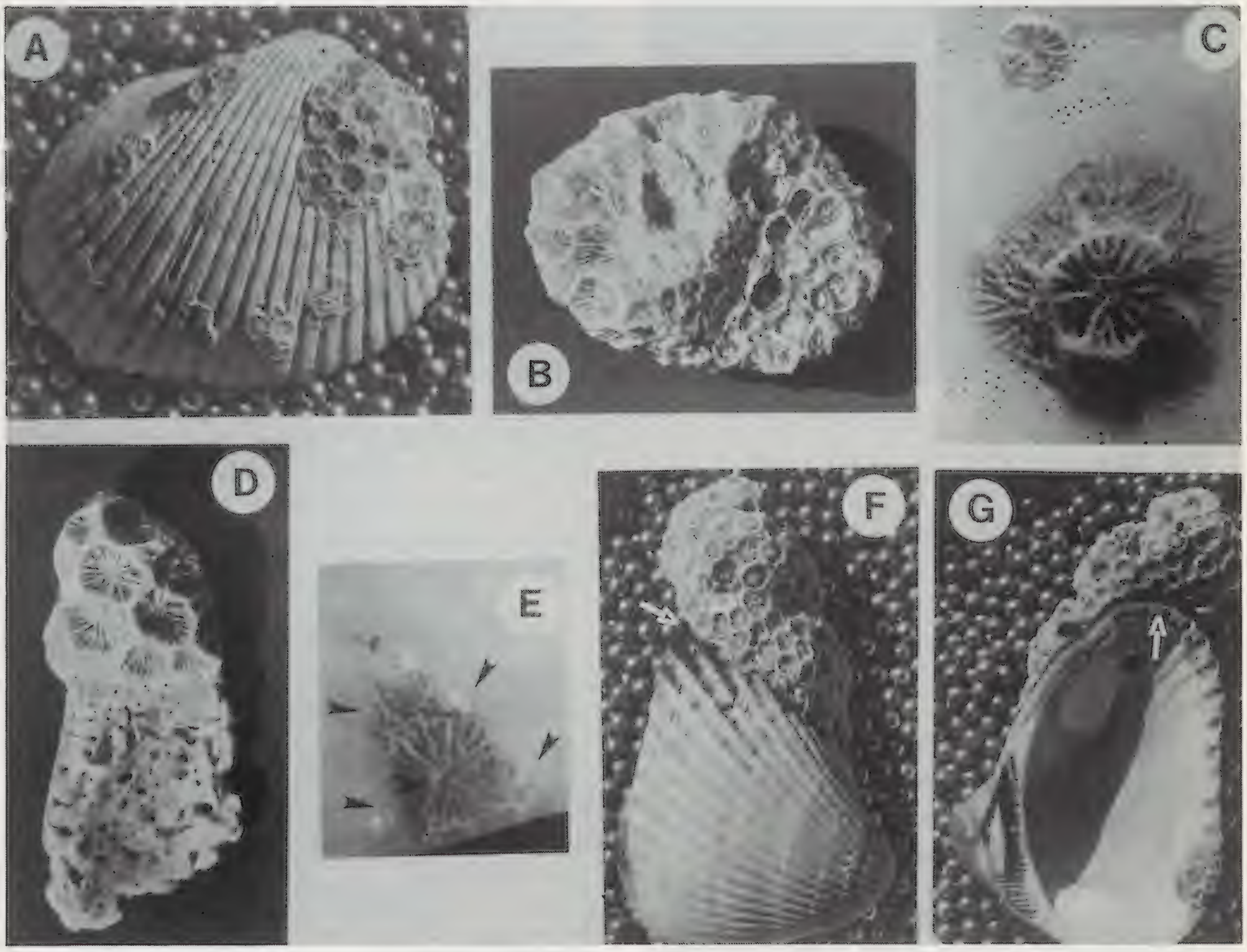

Figure 2. *Astrangia danae* from Pine Knoll Shores. A, Several small coralla on subfossil Holocene *Anadara* (shell is 59 mm in length). B, Corallum covering a patch of *Balanus* (specimen 36 mm across). C, Nascent colonies on interior of possible subfossil *Dinocardium* (largest corallite is 2.6 mm in diameter). D, Reworked Pleistocene shell fragment having a small, wrap-around colony (fragment 33 mm in longest dimension). E, Nascent colony in depression (arrows) on inside margin of *Anadara* (corallite 1.5 mm in diameter). F and G, Relatively large corallum on modern *Noetia*, overgrowing periostracum layer (arrows) (shell 66 mm in length).

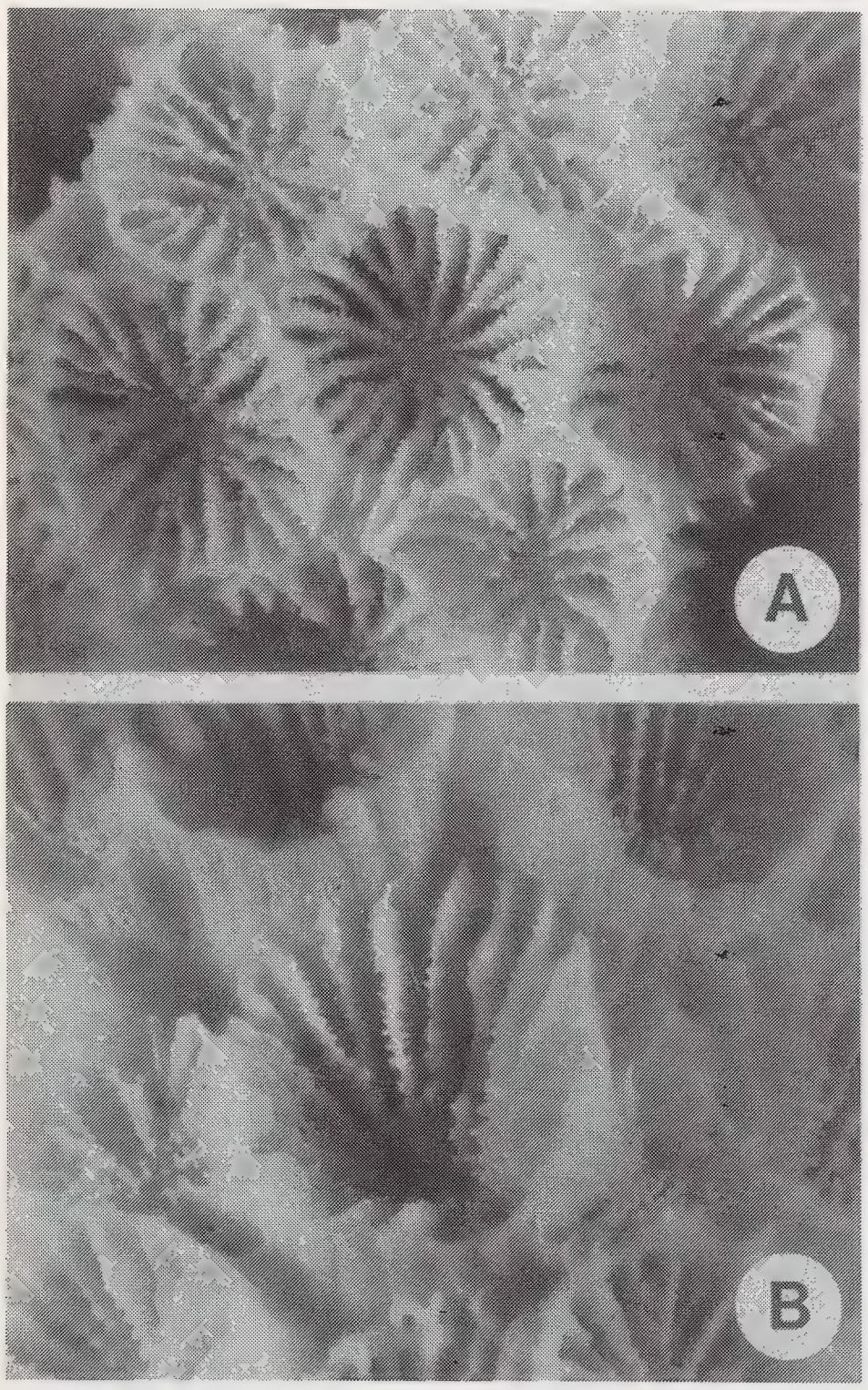

Figure 3. Morphologic variation in *Astrangia danae*. A, Closely-packed corallites (essentially cerioid organization). B, Corallites having raised margins (subplocoid organization). (Corallites in both photographs are 4 to 5 mm in diameter.)

TAPHONOMIC SIGNIFICANCE

A conspicuous feature of *A. danae* from Pine Knoll Shores is the excellent preservation of skeletal anatomy in many specimens, in contrast to the range of preservation quality exhibited by the more abundant molluscs. Other rare corals in the shell accumulations (?*Septastrea* sp.) are badly damaged and barely identifiable. This suggests that specimens of *A. danae*, at least at this particular site, probably are no older than Holocene and that most are derived from the modern nearshore zone.

Coralla of *A. danae* encrust a variety of shells, including Pleistocene estuarine shell fragments (Fig. 2D), Holocene subfossil marine shells (Fig. 2A), and modern marine shells with the periostracum still attached (Fig. 2F, G). All stages in corallum development are represented, from small incipient colonies (Fig. 2C) to large "columnar" colonies (Fig. 2F). Both inner and outer surfaces of mollusc shells are colonized; some nascent colonies are located in small cavities and depressions on the host shells (Fig. 2E). Colonies typically overgrow bored surfaces and epibiont patches (Fig. 2B, C and D), but are seldom overgrown or bored. Only a few coralla have been penetrated by clionid sponges and juvenile boring clams.

Substrata used by *A. danae* were not only derived from multiple sources, but also appear to have resided for varied time intervals at the seafloor. Some shells may have been buried and exhumed repeatedly (as in the "Jeram Model" of Seilacher, 1985). Occurrence of *A. danae* coralla representing all growth stages indicates that host shells were exposed from weeks to perhaps years at the continental shelf surface before being buried or transported to the foreshore. This demonstrates a complex interaction of a living sedentary, colonial organism with a variety of dead organisms over variable time spans. Although individual shell movement patterns and exact coral colonization environments are not known, Figure 4 depicts the most likely general pathways and environments involved.

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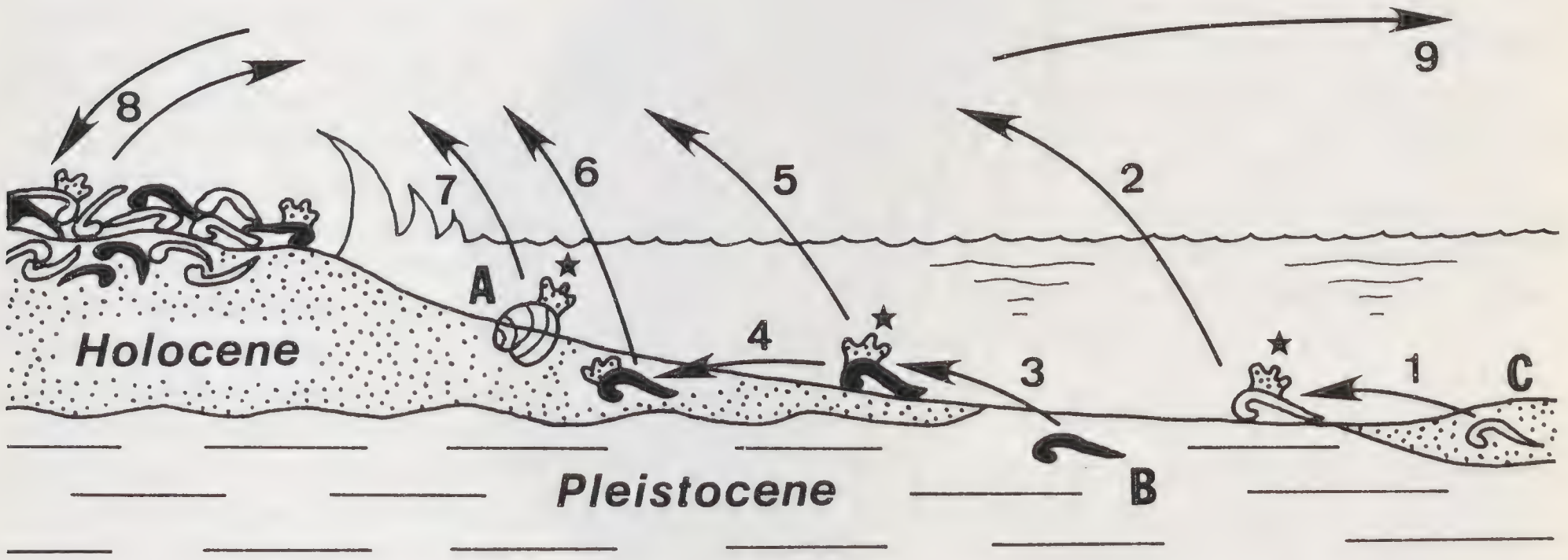

Figure 4. Possible transport pathways and colonization environments involving modern (A) and relict (B) host shells. 1, Exhumation of subfossil Holocene shells; 2, Holocene shells delivered to foreshore; 3, exhumation of Pleistocene shells; 4, reburial in Holocene shelf deposits; 5, Pleistocene shells delivered to foreshore; 6, Pleistocene shells undergo repeated burial and exhumation before being delivered to foreshore; 7, modern shells delivered to foreshore; 8, tidal cycles and storms move shells into and out of foreshore zone, probably many times; 9, export to deeper shoreface and offshore zones; and, ★, shells reside at seafloor long enough to be colonized or overgrown by *Astrangia danae*. (Not drawn to scale.)

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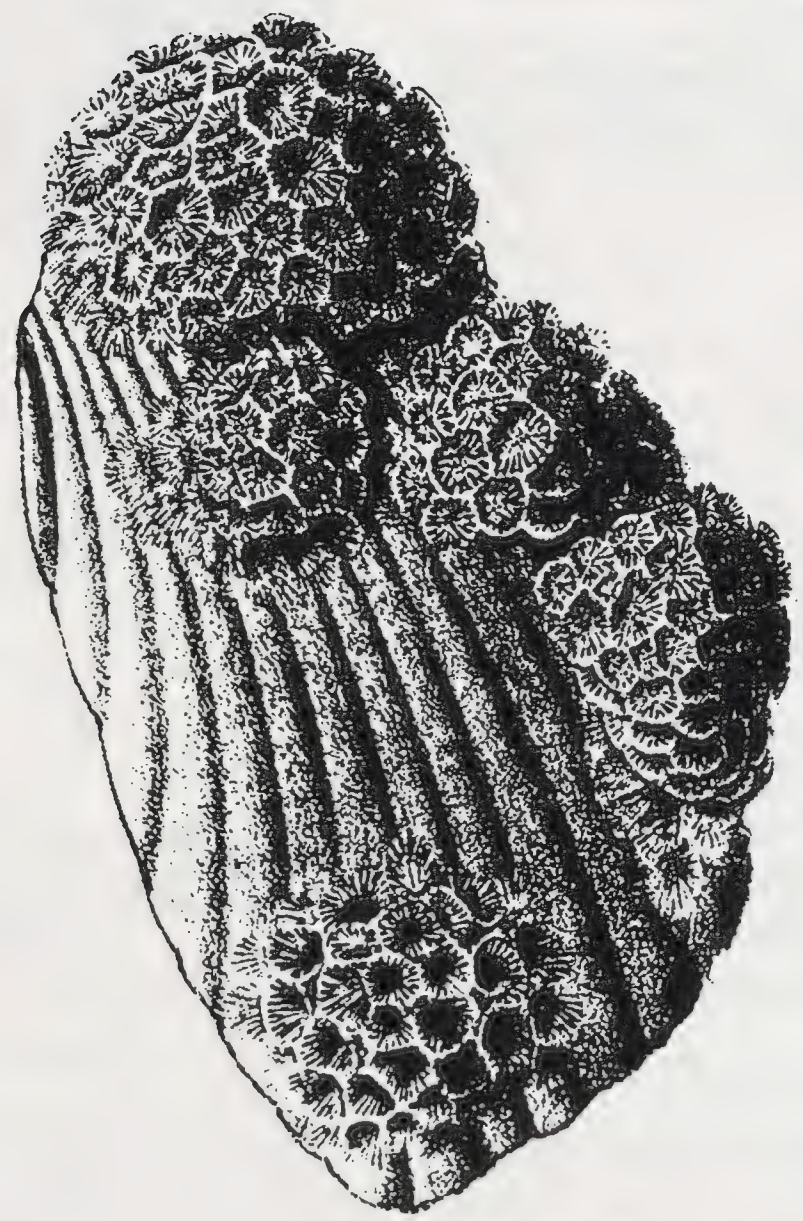

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PALYNOLOGICAL CHARACTERISTICS OF NEAR-SHORE SHELL-BEARING PLIOCENE THROUGH HOLOCENE SEDIMENTS OF FLORIDA, GEORGIA, AND SOUTH CAROLINA

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I. ABSTRACT

Seventeen pollen-bearing samples from sites in South Carolina, Georgia, and Florida were analyzed for their pollen content. The samples range in age from Late Pliocene to Holocene. The initial objective of the study was to use the samples to help define the age of the physiographic feature known as Trail Ridge. All samples were marine sediments, and many were from marine mollusk-dominated strata. Pollen of *Pinus* and *Quercus* were abundant in all samples; *Taxodium* was abundant in about half of them. *Carya, Liquidambar,* Compositae, Gramineae, and Chenopodiaceae-Amaranthaceae were present as accessory taxa. Dinoflagellate cysts, microforams, and pyrite were present, or abundant, in several of the samples. The only regionally extinct taxa were *Pterocarya* and *Sciadopitys* (?), and these were not abundant in any samples. The bio- and chronostratigraphic positions of the samples were established using mollusk, ostracode, and vertebrate fossil data, and radiocarbon dates where possible. In spite of the fact that the samples represent a considerable span of time (back to 2.2 million years) the pollen floras are very uniform. There is, for all practical purposes, no way of distinguishing the sampled Pliocene strata from the Pleistocene or Holocene units on the basis of pollen assemblages. The pollen floras seem to have been strongly influenced by taphonomic factors, such as sorting by wind, currents, and waves. Although this has nearly eliminated their value as biostratigraphic indicators, the pollen assemblages are useful indicators of a distinct kind of depositional setting. The taphonomic interpretation is corroborated by data derived from molluscan and vertebrate paleoecology.

II. INTRODUCTION

The research represented in this paper was associated with a long-standing project whose purpose it is to delineate the ages and environments of deposition of coastal sand ridges in the southeastern

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United States; most of those ridges are generally acknowledged to be of Pleistocene age. Geologists at Georgia Southern University, the E. I. DuPont de Nemours and Co. Florida Plant, and the U. S. Geological Survey have focused a great deal of attention on Trail Ridge, in particular. Trail Ridge is a prominent coastal plain sand body, which is believed to represent a stranded shoreline complex that formed in association with a very early Pleistocene or Pliocene high-stand of the Atlantic Ocean (Figure 1). Trail Ridge contains large, extensive economic deposits of heavy mineral sands, and so constitutes an important source of industrial minerals. It is principally this fact that draws the attention of most geologists to Trail Ridge, but as a land form it is also the object of scientific interest. Many papers have been written about the physical characteristics of Trail Ridge, its age, and economic significance (*e.g.*, Pirkle and Yoho, 1970; Pirkle, 1972; Pirkle, 1975; Pirkle, 1984). As a result of the efforts to delineate the age of Trail Ridge an investigation into the palynological characteristics of Late Cenozoic strata in South Carolina, Georgia, and Florida was begun. Through the process of comparing pollen assemblages from Trail Ridge to deposits that are known to be Holocene, Pleistocene, and Pliocene in age, discoveries have been made that have helped to demonstrate why Trail Ridge, and other deposits of similar age and origin are so difficult to date palynologically.

If we use Trail Ridge as a point of departure, lithostratigraphically, biostratigraphically, and temporally, one can see that a variety of sedimentary units lie in close proximity to it. For this paper Huddleston's (1988) stratigraphic nomenclature of the Miocene through Holocene lithostratigraphic units of the Georgia Coastal Plain was used. Furthermore, Huddleston's data were projected north into South Carolina, and south into Florida for the purpose of establishing nomenclatural and stratigraphic continuity within this paper. To the extent that it is possible, stratigraphic interpretations from geologists working in Florida (Scott, 1988; Webb *et al.*, 1989; Jones *et al.*, 1991; Hulbert *et al.*, 1995) were used to complement Huddleston's work.

III. AGES OF STRATA

In the broadest interpretation of strata associated geographically with Trail Ridge, there are two classes of sedimentary deposits: 1) older, mostly consolidated, marine strata, which display fair lateral continuity, and which developed as sea level and shorelines oscillated during the Miocene and Pliocene (*e.g.*, the Hawthorn Group); and 2) younger, largely unconsolidated, discontinuous bodies of sand and clay, which lie eastward of Trail Ridge and comprise a series of beach ridge/shoreline complexes that developed during the Pleistocene and Holocene (Figure 2).

Trail Ridge clearly lies on top of Miocene units, and apparently overlies Pliocene formations as well. The Principle of Superposition of Strata makes that intuitively obvious even if actual outcrops with lithologic contacts are rare or contacts are known only from the subsurface. Trail Ridge has a more tenuous stratigraphic relationship with the Pleistocene beach ridges, however, because one can demonstrate neither superposition of strata nor lateral continuity to establish concrete depositional or temporal relationships. It is logical to believe that Trail Ridge is older than, for example, the Penholoway Terrace Barrier (Figure 2; Hoyt and Hails, 1969). Trail Ridge lies furthest inland, and at the highest elevation, and so must have been deposited earlier than any of the other shorelines. That, however, is the most one can say with confidence. In order to increase the biostratigraphic resolution of the age of Trail Ridge, palynological analyses of a wide variety of samples from strata closely associated with Trail Ridge were undertaken for this study.

Rich (1985) published the results of pollen analyses of two cores of lignite from beneath the sands of Trail Ridge near Starke, Clay County, Florida (Figure 1). After comparing the pollen assemblages to those derived from other locations in the southeastern United States, it was concluded that the lignite-producing swamp and, hence, Trail Ridge could not be of Miocene age, but no further deliniation of age could be made. Further analysis of the stratigraphic and sedimentological relationships between Trail Ridge sands and

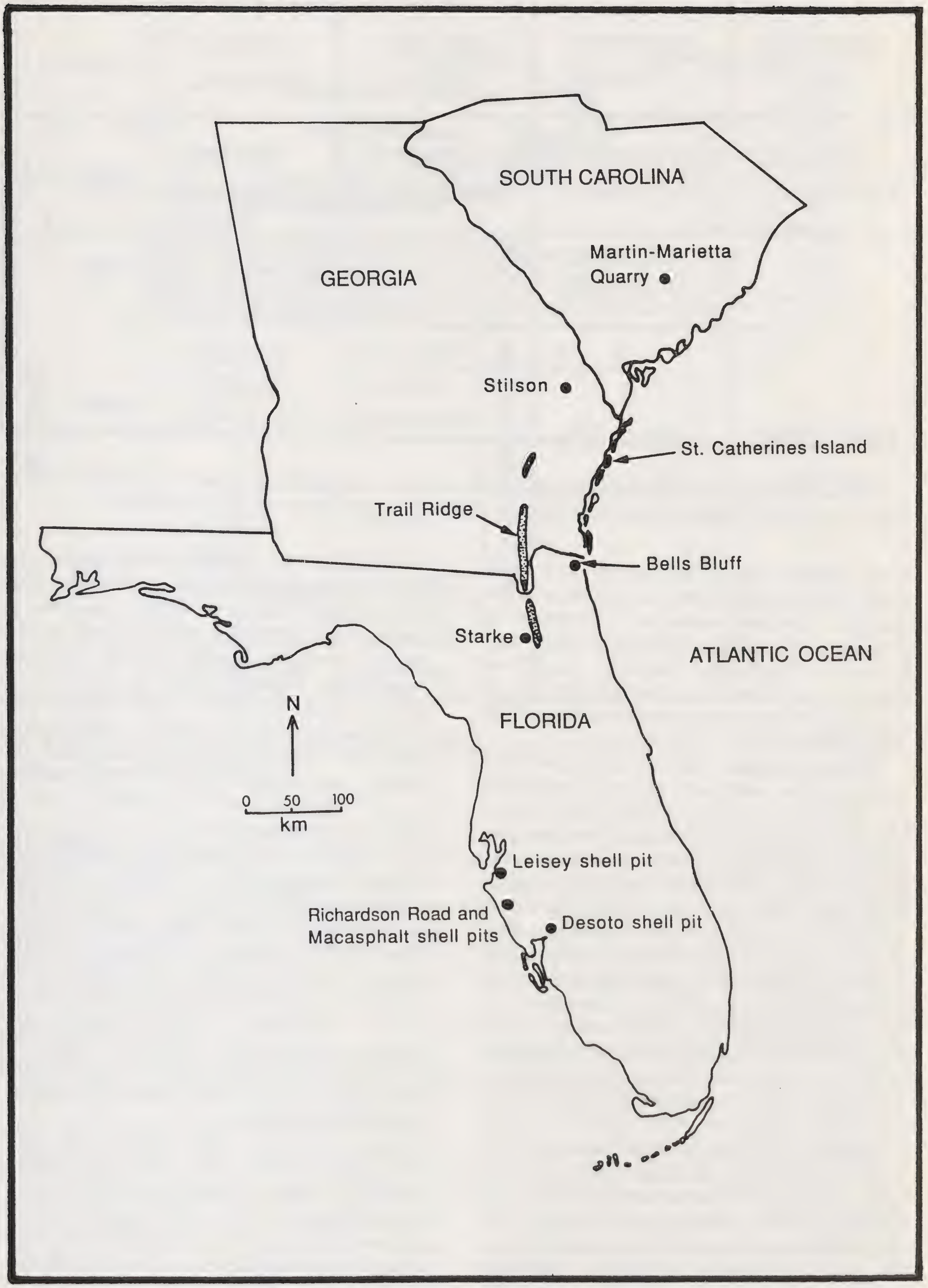

Figure 1. Location map of physiographic features and sample localities.

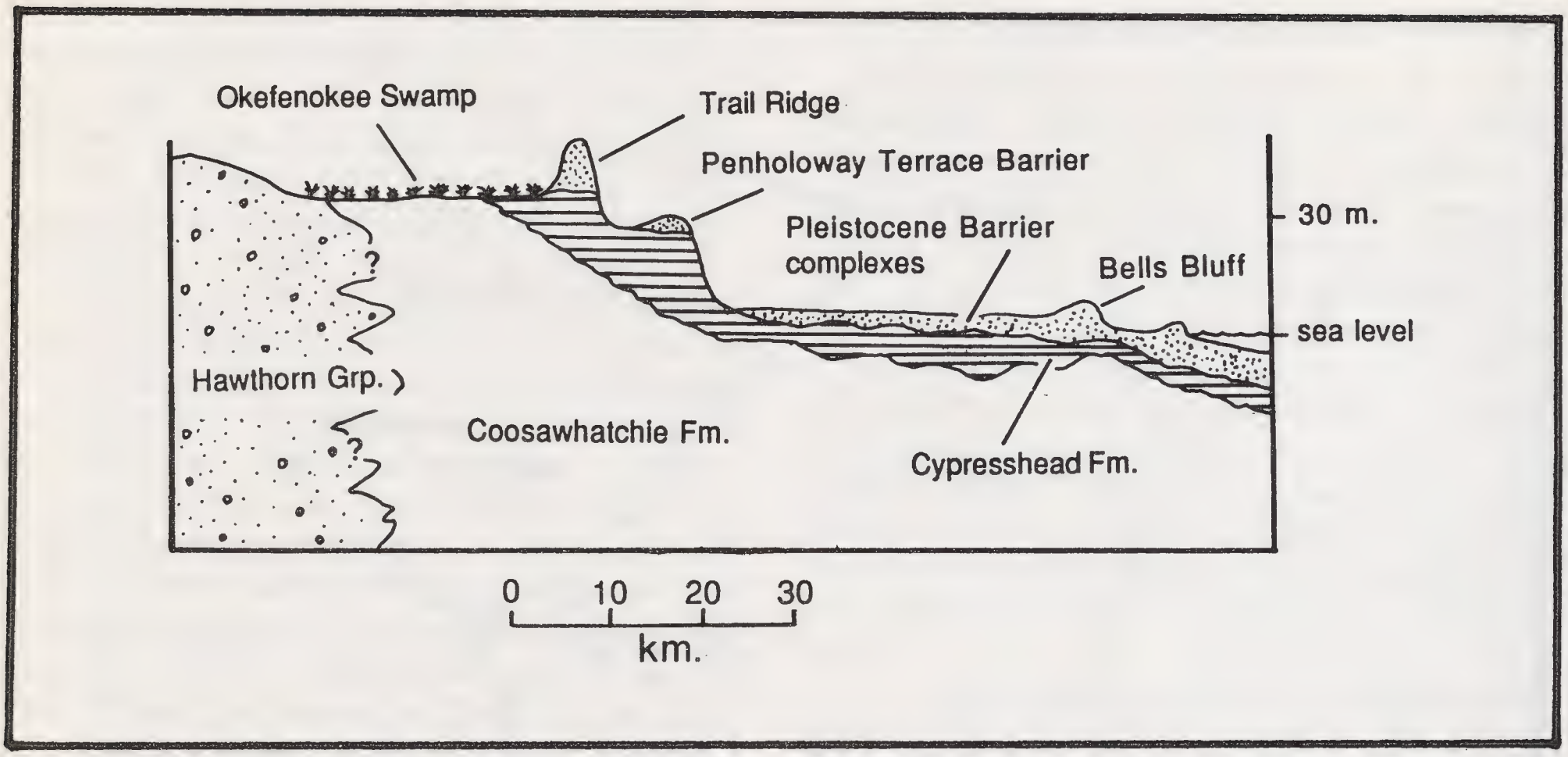

Figure 2. Generalized stratigraphic cross-section of strata lying beneath, and laterally adjacent to Trail Ridge (from Huddleston, 1988).

Trail Ridge lignite led Force and Rich (1989) to conclude that the deposits were indeed contemporaneous (representing dune sands, which gradually invaded and buried a freshwater swamp), but they found no evidence to constrain the age of the deposit with more precision than Rich did in 1985.

Pliocene strata – Inasmuch as the Trail Ridge pollen produced no clear indication of age (no extinct or regionally extinct taxa), a search was begun for samples which, based upon other criteria, were known to be of Pliocene age. It was hoped that something distinctive might be found in Pliocene samples from various locations that would serve as a common and distinctive identifier of Pliocene deposits in the southeastern United States. Tom Ager (U. S. Geological Survey, pers. comm., 1991) suggested that *Pterocarya* and *Sciadopitys* might be found in Pliocene strata, so those two genera were particularly sought in pollen preparations.

Samples of known Pliocene age were collected from four localities (Figure 1) and are as follows: 1) sediment in-filling of a large *Ecphora quadracostata* shell, collected from the Raysor Formation, Martin-Marietta limestone quarry, Berkeley County, South Carolina; 2) oyster in-filling from the Raysor Formation, Martin-Marietta quarry; 3) sediment in-filling from the shell of the oyster *Ostrea disparilis*, from the Raysor Formation, Stilson, Bulloch County, Georgia; 4) two samples of Macasphalt Shell Pit (also known as the APAC Shell Pit) matrix, Bed 4, Tamiami Formation, Sarasota County, Florida; 5) matrix from around a fossil camel jaw (*Hemiauchenia blancoensis*), Macasphalt Shell Pit; and 6) four samples from the Quality Aggregates Shell Pit (also known as the Richardson Road Shell Pit) in Sarasota County, Florida.

According to Huddlestun (1988) the Raysor Formation immediately underlies the Cypresshead Formation (shown in Figure 2) where the two units occur together. Ward and Huddlestun (1988) state that the Raysor "is a facies equivalent of the shelly, quartzose sands of the Yorktown Formation in northeastern South Carolina and southeastern North Carolina." Planktonic foraminifera indicate a late Pliocene (early Piacenzian) age for the Raysor Formation (Huddlestun, 1988).

Deposits from the shell pits near Sarasota, Florida, have been ascribed a variety of ages, something which Jones *et al.* (1991) point out in their paper. Part of the problem of dating the shell beds stems from the fact that they are laterally discontinuous, and there are many different shell accumulations along the Gulf coast of Florida. Petuch (1982) has described 11 stratig-

SERIES		E. SOUTH CAROLINA	EASTERN GEORGIA		NORTHERN FLORIDA	SOUTHERN FLORIDA
PLIOCENE		RAYSOR FORMATION	CYPRESSHEAD FORMATION		CYPRESSHEAD FORMATION	TAMIAMI FORMATION
MIOCENE	upper				REWORKED SEDIMENT	
	middle	COOSAW-HATCHIE FORMATION	COOSAW-HATCHIE FORMATION	HAWTHORN GROUP	HAWTHORN GROUP	HAWTHORN GROUP
	lower	MARKS HEAD FORMATION	MARKS HEAD FORMATION			
		PARACHUCLA FORMATION	PARACHUCLA FORMATION			

Figure 3. Formational correlations in selected areas of the Georgia and Florida coastal plains (from Scott, 1988).

raphic units at the Macasphalt Shell Pit; beds 9-2 comprise what are known as the Pinecrest Beds. The Macasphalt samples described in this paper all come from Petuch's Unit (or Bed) 4 of the Pinecrest Beds of the Tamiami Formation. According to Scott (1988; Figure 3) the Tamiami Formation is stratigraphically equivalent to the Raysor Formation.

Jones *et al.* (1991) provide data on ostracodes from the Macasphalt Shell Pit that show a correlation between Units 10-5 at Macasphalt and ostracode-bearing horizons in the Raysor Formation in Georgia. Even though the Unit 4 Macasphalt samples described in this paper are slightly younger than the Raysor Formation, the general stratigraphic equivalence of the beds suggests a close depositional and temporal relationship between the Tamiami and Raysor Formations.

Most of the shell beds that make up the Pinecrest Beds are incredibly fossiliferous, bearing well-preserved individuals which, according to Jones *et al.* (1991), represent 200 species of bivalves, 600 species of gastropods, and perhaps as many as 100 species of vertebrates, including 19 taxa of land mammals. Unit 4 sediments differ from the rest of the Pinecrest beds in that the fine-grained, organic-rich sands, which constitute Unit 4, contain predominantly a brackish (not normal marine) molluscan and ostracode fauna as well as land and freshwater vertebrates and gastropods (Jones *et al.*, 1991; Ward, 1992). Peculiar among the many vertebrate species in the Pinecrest Beds are nearly 40% representing birds; one horizon discovered at the Quality Aggregates Shell Pit, near the Macasphalt locality, contains an unusual concentration of cormorant skeletons

(*Phalacrocorax* sp.; Emslie and Morgan, 1994). The terrestrial mammals offer the best vertebrate biochronology for the Macasphalt site (Morgan and Hulbert, in press). These include characteristic taxa of the Late Blancan North American Land Mammal Age (NALMA; Figure 4), such as *Nanippus peninsulatus* (a three-toed

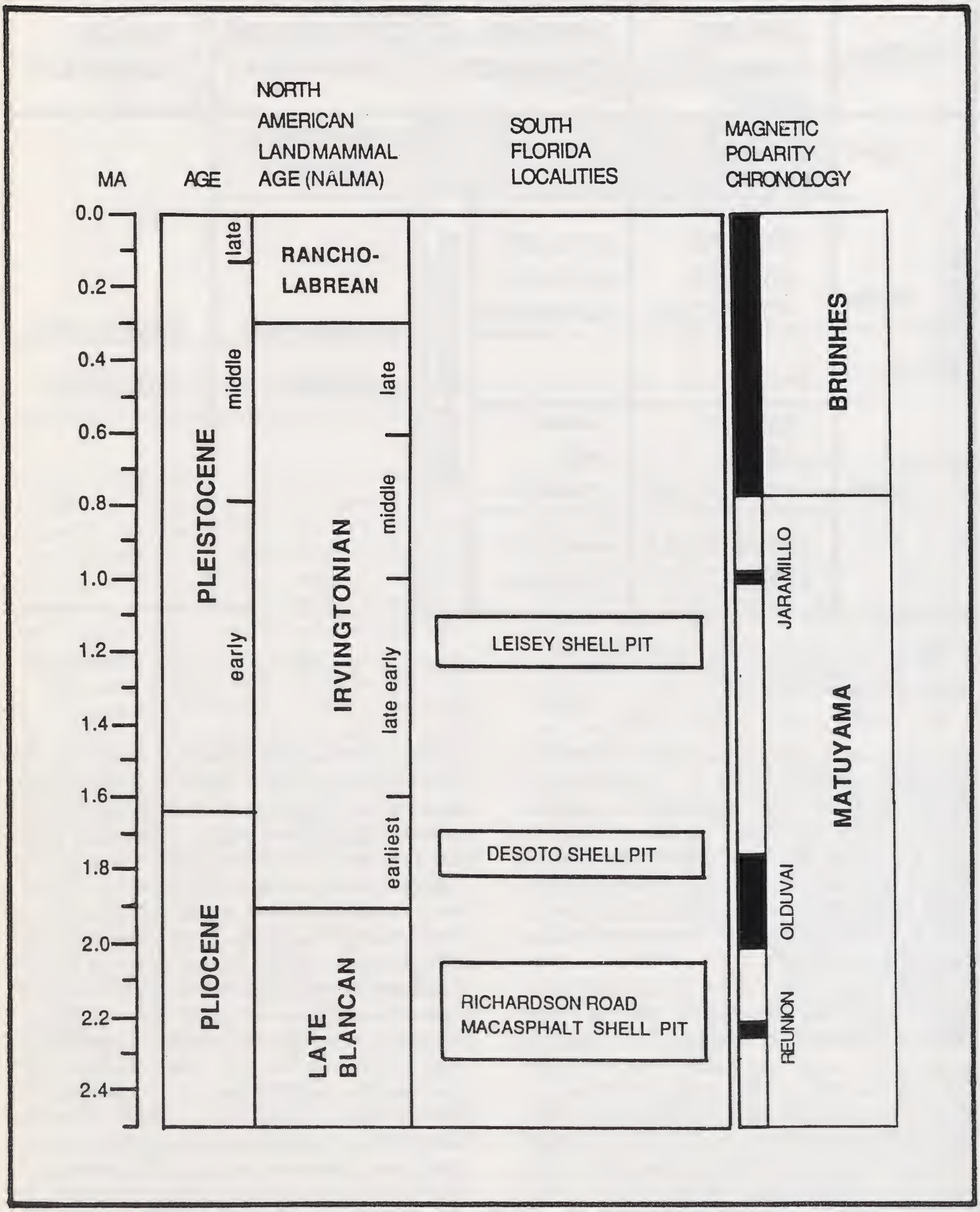

Figure 4. Correlation of vertebrate fossil sites discussed in this paper with North American Land Mammal Ages, geologic ages, and magnetic reversals (after Morgan and Hulbert, 1995).

horse), *Megalonyx leptostomus* (a ground sloth), *Neochoerus dichroplax* (a capybara), *Geomys propinetis* (a pocket gopher), and *Sigmodon medius* (a cotton rat).

Earliest Pleistocene Strata – The earliest Pleistocene strata dealt with here are from the Desoto Shell Pit, Desoto County, Florida, and the Leisey Shell Pit, near Tampa, Florida, (Figure 1). The Desoto deposit accumulated during the latest Pliocene/earliest Pleistocene (Figure 4) and is associated with the Caloosahatchee and Bermont formations (Willard *et al.*, 1993).

The Leisey Shell Pit is another spectacular accumulation of marine invertebrate shells, terrestrial and aquatic vertebrate remains, and plant fossils (Hulbert *et al.*, 1995) which come from the Bermont and Fort Thompson formations. Nearly 30,000 catalogued vertebrate specimens alone have been recovered, and represent over 100 species. Hulbert *et al.* (1995) present detailed and convincing arguments based upon vertebrate biochronology, strontium isotope chronology, and magetostratigraphy to constrain the age of the Leisey deposits to the early Pleistocene (Figure 4). Chronologically useful mammalian taxa present at Leisey include *Mammathus hayi* (a primitive mammoth), *Smilodon gracilis* (a saber-toothed cat), *Canis edwardsii* (a small wolf), *Canis armbrusteri* (a larger wolf), and *Sigmodon libitinus* (a cotton rat) (Hulbert and Morgan, 1987; Morgan and Hulbert, 1995). The two Leisey samples described here came from excavations identified as pits 1A and 3A (see Morgan and Hulbert, 1995, Figure 1) and consist of fine-grained sandy matrix preserved inside mollusk shells.

Late Pleistocene Strata – A large number of late Pleistocene samples have been analyzed from various locations on the Atlantic Coastal Plain in Georgia and Florida. A locality, which has recently received attention, and which lies near the town of St. Marys, Georgia, is Bells Bluff. The fossiliferous shoreline strata of Bells Bluff include a shell-rich horizon, which lies at sea level. Rich and Pirkle (1993) reported that shells of *Anadara* sp. from Bells Bluff were radiocarbon dated at 37,395 $\pm$ 2155 years BP. The samples analyzed for this project consist of sandy shelly sediment, which was washed from within two large cockles (*Dinocardium* sp.) that were collected along with the *Anadara*.

Holocene Strata – Two Holocene samples were chosen for comparison with the Pliocene and Pleistocene sediments, and were selected because of their compositional similarities to the older samples. Both Holocene samples were collected on St. Catherines Island, immediately off the Georgia coast (Figure 1). The seaward side of St. Catherines Island has well-preserved deposits of peat and shells, which have been exposed by erosion in recent years. Among the shell beds is a bed of oysters (*Crassostrea* sp.) exposed at a site known as South Beach. Shells, and the blue mud that encloses them, were collected and sampled for pollen analysis. Shells of clams and mussels, and peat from a nearby location have been dated, and suggest that the oyster bed accumulated about 600 years BP.

The second of the Holocene samples, also from St. Catherines Island, was recovered from a core taken near Cracker Tom Hammock, inland of the oyster bed. The sample consisted of *Crassostrea* shells in a sandy clay matrix, and came from a depth of 1.9-2.2 meters. Shells from the deposit have been radiocarbon dated at 3202 $\pm$ 73 years BP.

IV. PROCESSING TECHNIQUE

Most of the sediments were sandy carbonate-rich muds; the Leisey, Desoto, Macasphalt, Raysor, Bells Bluff *Dinocardium,* and Cracker Tom samples consisted of mollusk shell-dominated sandy clays. One Desoto sample included matrix from a tortoise shell fossil. The South Beach *Crassostrea* and Bells Bluff clay samples were both smooth, blue, plastic, carbonate-rich clays. The shell pit samples were carefully selected from the plastic bags they had been stored in, and were scraped and washed thoroughly so as to remove surface contaminants. Where large shells were found (*e.g.*, planispiral gastropods 1-2 cm across) the shell contents were washed out and processed. In the case of the *Ecphora* and *Dinocardium* in-fillings the entire contents of the shells were washed from the specimens, small shell fragments were sieved out, and the fine-grained residues were further treated. Each of the samples

was placed first in 10% HCl to remove carbonates. Most of them reacted vigorously, and the shell pit samples all gave off a pronounced odor of petroleum. Samples that were clearly organic-rich were then mixed with 10% KOH and placed in a boiling water bath for 10 minutes to dissolve soluble organic substances. After thorough washing to remove the soluble organic fractions, the residues were placed in concentrated HF to remove silicates. After remaining in the HF for several days (in most cases), processing was terminated and the residues were mixed with a 50:50 blend of water and glycerine jelly. Several microscope slides were prepared for each of the 17 samples and a minimum of 200 identifiable grains was counted for each sample. Counts were made by observing the slides with a Jena research photomicroscope.

V. RESULTS OF THE ANALYSES

Gross characteristics of the acid-insoluble residues were much the same from one deposit to another. Organic fragments were usually small, and pine pollen (*Pinus* spp.), which were invariably present, were oftentimes broken in halves. Pyrite was typically present, either as minute cubes or as tiny framboids. Dinoflagellate cysts, especially the round, spiney, chorate type (Plate 1) were usually present, and sometimes dominated the samples. Dinoflagellates were particularly common in the Leisey shell pit samples, as well as the *Ecphora* in-filling from the Raysor Formation, and the Macasphalt samples. Microforams were present as well; these minute, pseudochitinous internal test linings were described by Cohen and Gruber (1968) and are common in pollen preparations derived from sediments that have experienced marine influence.

The dinoflagellates and microforams clearly are contributions of the marine environment and their uniformity of expression is not surprising. Although pyrite may be generated within sediments derived from a variety of environments, the abundance of pyrite also seems to be a reliable indicator of marine deposition (see Blatt *et al.*, 1980, for a related discussion). The pollen from land plants also was represented uniformly, however. *Pinus* and *Quercus* (oak; Plate 1) tended to dominate all samples, ranging to as high as 45-60% for *Pinus* and 25-30% for *Quercus* (Figure 5). *Taxodium* (cypress) was also abundant in about half the samples (from the Richardson Road locality, in particular), with relative abundances on the order of 6-39%. Anyone who has worked much in the southeastern United States is familiar with the dominance of *Pinus*, *Quercus*, and *Taxodium* in most pollen assemblages (*e.g.*, Watts, 1969, 1971; Cronin *et al.*, 1981). Willard *et al.* (1993) also mention this fact in a paper wherein they describe the pollen floras from three Pliocene-Pleistocene sites in southwestern Florida. It is the pollen that are the accessories to these major constituents, which seem to bear more careful consideration, however. *Carya* (hickory/pecan) and *Liquidambar* (sweet gum) were typically present in amounts of only a percent or two, but they were usually present in the samples analyzed for the current study [Willard *et al.* (1993) also recorded *Carya* in their work]. Other woody taxa, including *Alnus* (alder), *Ulmus* (elm), and *Nyssa* (black gum) accompanied these trees in variable amounts. These were much less common, however. Herbaceous pollen, which were almost invariably present in the samples, include Gramineae (grasses) and Compositae (asters and their kin), and Chenopodiaceae/Amaranthaceae (chenoams); the Leisey 3A sample had nearly 30% of the latter, while the Desoto tortoise sample had 46%, a very high percentage. Some samples also contained freshwater algal remains such as *Botryococcus* colonies or, more rarely, *Pediastrum*.

Among the pollen assemblages derived from samples known to be of Pliocene age, there were none that, based upon the occurrence of extinct species or otherwise

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PLATE 1

Selected pollen found various sample sites: 1) *Pinus*; 2) *Taxodium*; 3) *Quercus*; 4) *Carya*; 5) *Liquidambar*; 6) *Pterocarya*; 7) *Sciadopitys*; 8) dinoflagellate cyst. All figures are the same magnification; the bars represent 10 microns. Figures 1-5 were fresh pollen, figures 6-8 were fossilized.

PLATE 1

unusual taxa, were clearly of Pliocene age. Occasionally a grain of *Pterocarya* (5 of 11 Pliocene samples), or what appears to be *Sciadopitys* (2 of 11 Pliocene samples; Plate 1) was found in samples that were by other means known to be Pliocene, but neither genus was abundant and their occurrences were not consistent from one Pliocene sample to another (Figure 5). Ager (personal communication, 1995) has noted that only a few grains of *Pterocarya*, in particular, may be associated with deposits which have numerous leaf and seed fossils of the genus (*e.g.*, the Late Miocene Brandywine deposit; McCartan *et al.*, 1990), so modest amounts of the pollen may not reflect the actual abundance of the plants near the site of sediment accumulation. This is also true of the related genus *Carya* whose plants are extremely abundant in the southeastern United States (particularly the pecan, *Carya illinoensis*), yet whose pollen are not especially common in sediments. The actual significance of just a few grains of *Pterocarya* and *Sciadopitys* pollen in Pliocene strata needs to be better defined.

VI. INTERPRETATION OF THE DATA

What was discovered among the samples that were observed is uniformity, both stratigraphically and geographically. The reader should recall that the intention of this study was to identify an assemblage of pollen, spores, or other palynomorphs that could be used to distinguish Pliocene deposits from Pleistocene deposits in the southeastern United States. Many authors, including Traverse (1988) have shown that pollen and spore assemblages constitute very valuable and sensitive biostratigraphic markers and usually can be relied upon to provide excellent biostratigraphic information. In the case of the current study, however, biostratigraphy seems to have lost some of its utility. Among other things, the apparent lack of regionally extinct taxa in Trail Ridge sediments has prevented assigning an age to that deposit based upon biostratigraphic evidence. The problem remains in that, after surveying 17 samples representing similar nearshore depositional environments from Pliocene, Pleistocene, and Holocene deposits from the southeastern United States, all that is found is a pollen flora which appears again and again. One only rarely finds an exotic grain, and even then its history is in question because one cannot be certain that it has not been reworked. Were it not for the presence of two *Pterocarya* and five probable *Sciadopitys* grains in the Raysor Formation *Ecphora* in-filling, its residue would be nearly identical to the Quaternary clam and oyster-dominated sediments from Reids Bluff and St. Catherines Island. The presence of these regionally extinct genera should not be taken in and of itself as sound evidence of a Pliocene age, however. An abundant source of easily erodable sediments of pre-Pliocene age exists in the southeastern states, and pollen derived from those older strata could be readily reworked into younger material.

Even if the problem of resolving the age of Trail Ridge remains, something else that is of palynological interest has been discovered. What was identified is not a pollen flora that has much biostratigraphic value, but one that has taphonomic and environmental significance. It is a product of mixing of marine and terrestrial elements on a microscopic level. The pollen of regionally common terrestrial plants, mixed with the remains of freshwater algae and marine microfossils appear as a distinct assemblage. The fact that the pine pollen, in particular, are usually broken is suggestive of long distance transport in water, probably including abrasion and mechanical weathering by waves. The recognition that

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Figure 5. Relative abundances of pollen and spores from the samples included in this study; the zero value lies at the base line for each taxon and abundance increases to the right. This graph shows only those taxa with abundances of 1% or less in all samples. The top ten rows of specimens came from sites known to be of Pliocene age. Richardson Rd. = Richardson Road locality; Bells Bluff *Dino.* 89 and 91 = *Dinocardium* in-fillings collected in 1989 and 1991, respectively; St. Cath. S. Beach = St. Catherines Island South Beach sample, and St. Cath. C. Tom = St. Catherines Island Cracker Tom Hammock sample.

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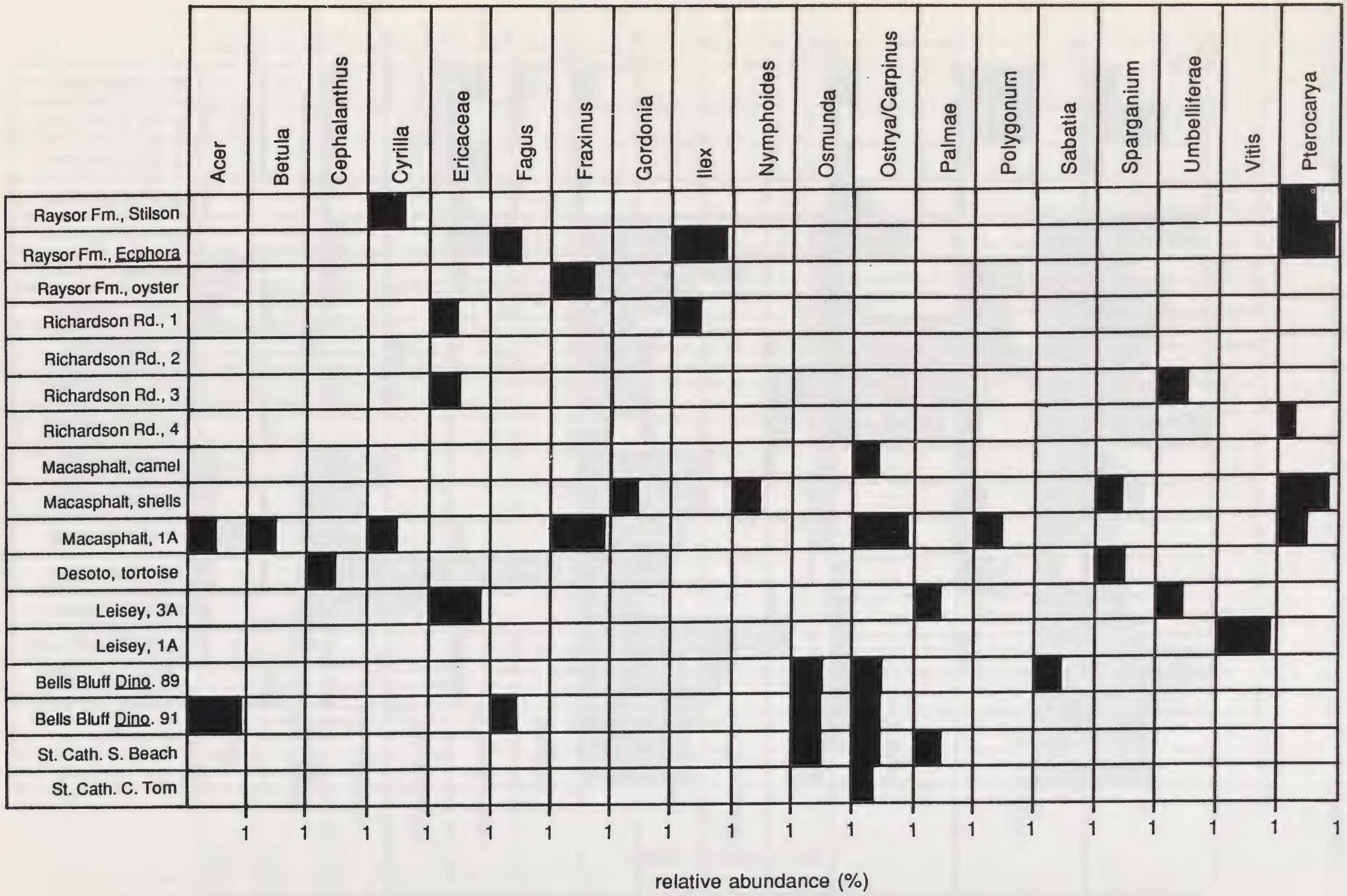
Acer
Betula
Cephalanthus
Cyrilla
Ericaceae
Fagus
Fraxinus
Gordonia
Ilex
Nymphoides
Osmunda
Ostrya/Carpinus
Palmae
Polygonum
Sabatia
Sparganium
Umbelliferae
Vitis
Pterocarya
Raysor Fm., Stilson
Raysor Fm., Ecphora
Raysor Fm., oyster
Richardson Rd., 1
Richardson Rd., 2
Richardson Rd., 3
Richardson Rd., 4
Macasphalt, camel
Macasphalt, shells
Macasphalt, 1A
Desoto, tortoise
Leisey, 3A
Leisey, 1A
Bells Bluff Dino. 89
Bells Bluff Dino. 91
St. Cath. S. Beach
St. Cath. C. Tom
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
relative abundance (%)

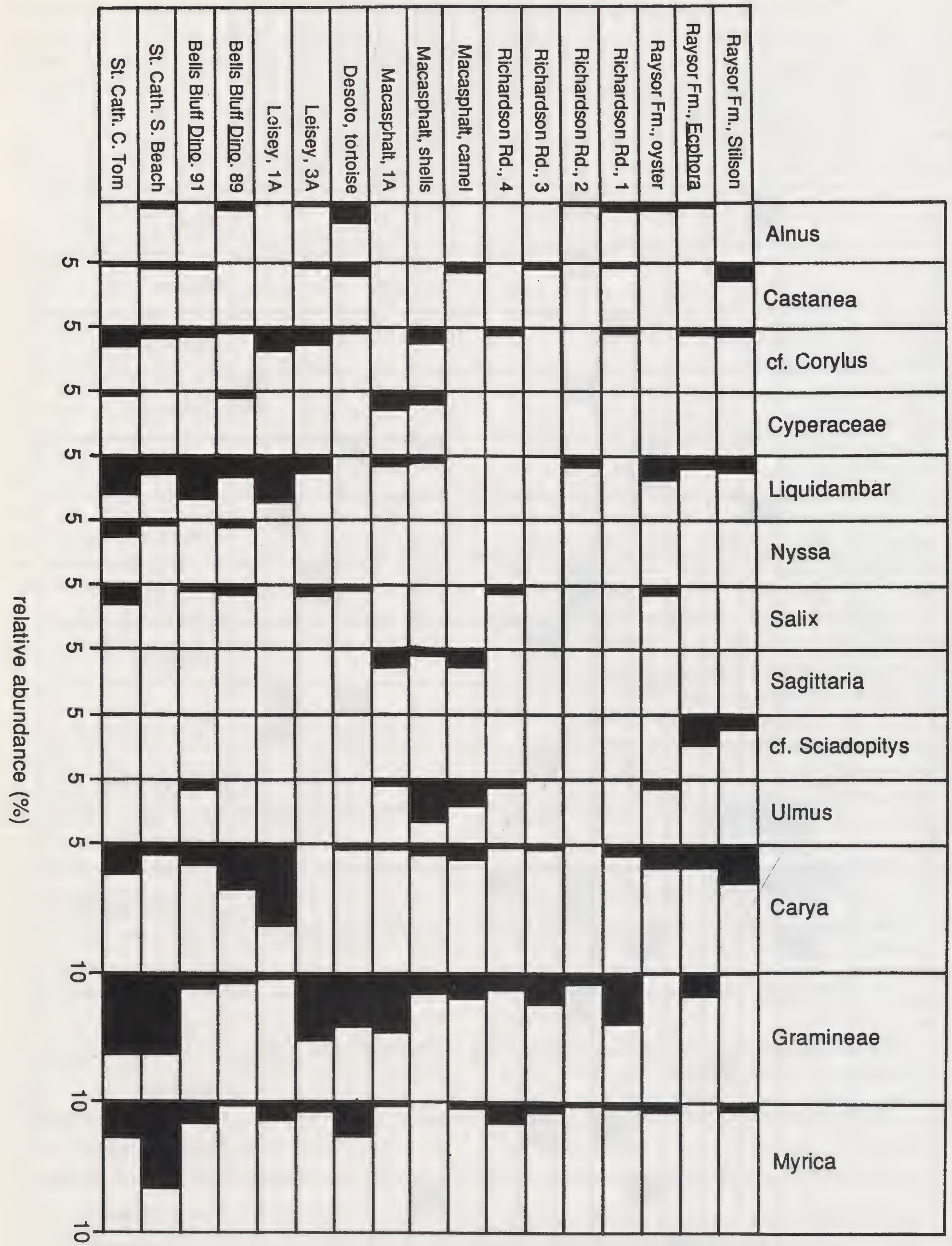

Figure 5, cont. Relative abundances of pollen and spores which, if present, constitute as much as 5% or 10% of the total in all samples.

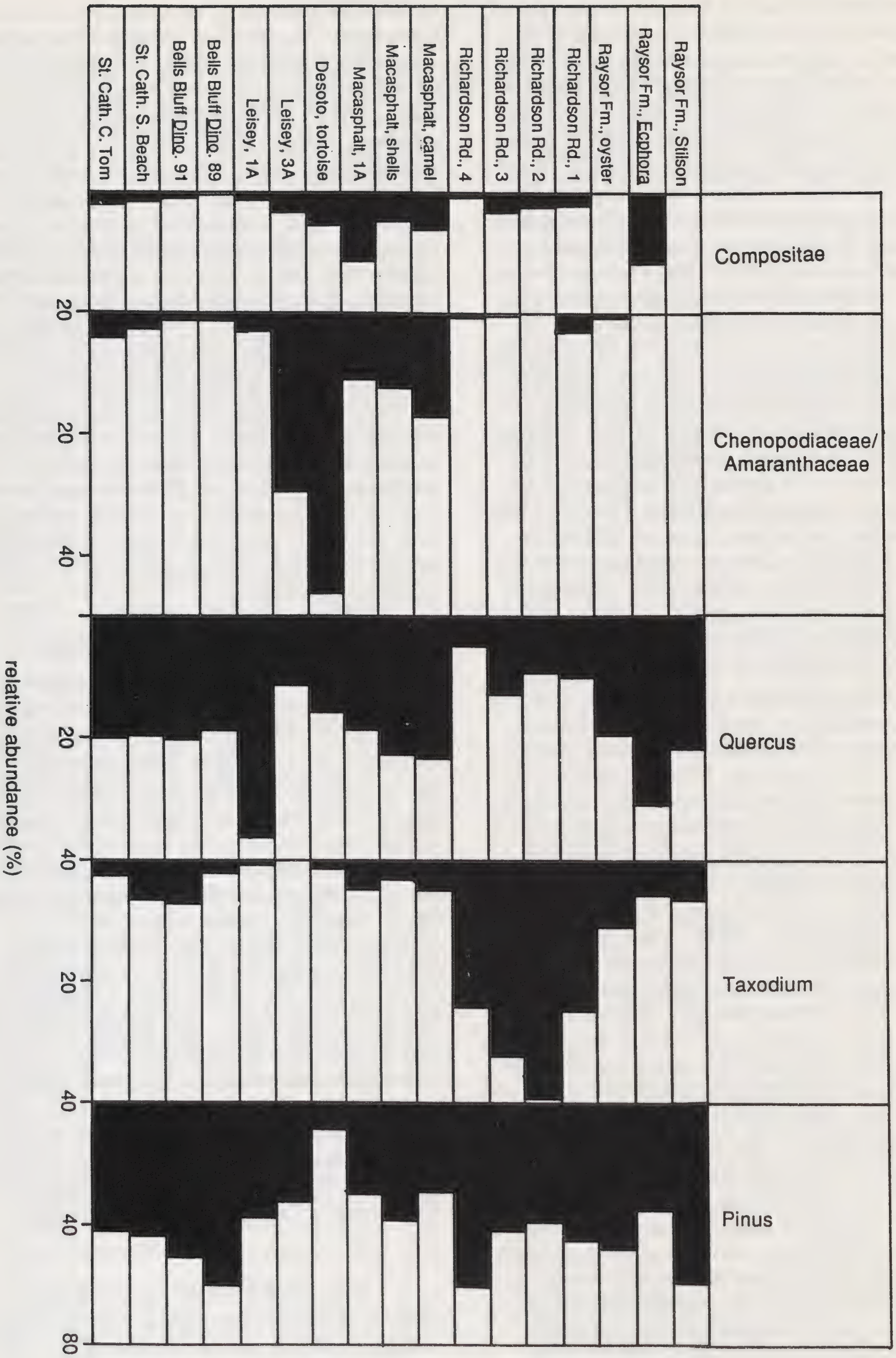

Figure 5, cont. Relative abundances of pollen and spores which, if present, constitute as much as 20%, 40%, 50%, or 80% of the total in all samples.

the deposits contain a blend of marine or brackish and freshwater or terrestrial fossils comes quite independently of the results of work performed by Richard Hulbert, a vertebrate paleontologist who has worked on all of the mentioned Florida localities. In a 1987 paper, wherein Hulbert describes a new species of the horse *Cormohipparion,* he presents the following description of the environment of deposition of the Macasphalt Shell Pit, Unit 4. It was "low energy shallow brackish water, rich in fluvial-derived organic sediments . . . The abundant siren, frog, and aquatic snake vertebrae are frequently complete, suggesting minimal transport, as do the numerous complete elements of the aquatic avifauna." Hulbert's environmental interpretation can be generally applied to the Leisey, St. Catherines Island, Desoto, and Bells Bluff localities, though there are chacteristics of each site that make them unique. The Raysor Formation and Leisey samples probably represent more open, normal marine deposits, but the fact that they accumulated under coastal conditions is the most important consideration.

The realization that certain pollen assemblages reflect sedimentary facies is not a new one, certainly. Wilson (1971) illustrated the relationship between distance from shore and relative abundances of different species of pollen as he described depositional environments for the Carboniferous of Oklahoma. Brush (1988), Brush and Brush (1994), and Rich and Pirkle (1994) have similarly studied the distributions of pollen taxa along the Atlantic seaboard of the United States. What makes the current study interesting, I believe, is the fact that, by separate means, employing very different kinds of fossils, a vertebrate paleontologist and a palynologist have come to the same conclusion regarding the environments of deposition of Pliocene strata in the southeastern United States. It might be argued that the same interpretations could be drawn from the abundant mollusk or ostracode remains, and that those fossils, furthermore, also provide a high degree of age resolution. This is certainly true, where the invertebrate remains are abundant. The abundance of invertebrate remains, such as are present at the Macasphalt, Leisey, Stilson, or Martin-Marietta sites is highly unusual, however. One is most likely to find a few scattered shell fragments, and a great deal of sediment that has no visible fossil contents. Under those circumstances, knowing that there is, potentially, a useful assemblage of pollen that can be used to define environment of deposition, one can proceed with paleoenvironmental interpretations with a fair degree of confidence. There is likely to be a very strong taphonomic overprint in such strata; the principle reasons why Pliocene sediments cannot be distinguished from Early or Late Pleistocene, or Holocene strata seems to be that, 1) the vegetation has remained stable for a long time, with the constituent species being affected little or none by the well-known periods of Pleistocene climatic cooling and 2) sorting by waves, currents, and, probably wind have lead to the preferential near-shore deposition of a distinct assemblage of taxa.

VII. ACKNOWLEDGMENTS

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NOTES ON THE FAUNA OF THE CHIPOLA FORMATION–XXXVIII TWO NEW SPECIES OF THE GENUS *TURBO* (GASTROPODA:TURBINIDAE)

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According to Hickman and McLean (1990, p. 57), the genus *Turbo* first appears in Upper Cretaceous rocks and reached its highest level of diversity in the Cenozoic. Today, members of this genus thrive in shallow tropical and subtropical marine environments where they have a strong affinity for calcareous substrates (Hickman and McLean, 1990, p. 57).

Examination of Chipola Formation fossils has revealed the presence of two new species of *Turbo*. Both species were found in association with coral reef deposits along the Chipola River and Farley Creek. In addition, two opercula belonging to the genus *Turbo* were found in the Tulane collection. Both appear to belong to the same species, but neither was collected in association with a shell. One was obtained from TU 1048 and the other from TU 555. Both opercula are illustrated in Plate 1 (figures 4 and 5).

Family TURBINIDAE Rafinesque, 1815
Genus TURBO Linnaeus, 1758

Turbo LINNAEUS, 1758, Systema Naturae, ed. 10, p. 761.

Type species: *Turbo petholatus* Linnaeus, 1758, by subsequent designation, Montfort, 1810.

Subgenus HALOPSEPHUS Rehder, 1943

Halopsephus REHDER, 1943, Proc. Biol. Soc. Washington, v. 56, pp. 41-46.

Type species: *Turbo pulcher* Rehder, 1943, by original designation (*T. pulcher* Rehder, 1943, *non T. pulcher* Dillwyn, 1817 = *T. haraldi* Robertson, 1957).

TURBO (HALOPSEPHUS?) CHIPOLANUS Schmelz, n. sp.
Plate 1, figures 1, 2

Description: Shell medium-sized, turbinate in form, imperforate. Protoconch planate, glossy, about two whorls. Postnuclear whorls five; suture distinct. Aperture rounded, columellar portion thickened and slightly reflexed anteriorly. First three teleoconch whorls shouldered, remainder rounded. Faint, beaded spiral cords cover first three teleoconch whorls and adapical end of penultimate whorl. Body whorl and abapical end of penultimate smooth, except for numerous faint oblique growth lines. Well-preserved specimens with rows of dark spots on teleoconch whorls, as well as vertical, wavy, dark and light bands.

Holotype: USNM 484398; height 19.4 mm, maximum diameter 16.4 mm.

Type locality: TU 555, Chipola Formation, east bank of Chipola River, about 1,000 feet above Fourmile Creek (SW 1/4 Sec. 29, T1N, R9W), Calhoun County, Florida.

Paratype: USNM 484399; height 22.6 mm, maximum diameter 19.0 mm; locality TU 555, east bank of Chipola River, about 1,000 feet above Fourmile Creek, Calhoun County, Florida.

Additional unfigured paratypes: Five specimens from TU 555 (Tulane collection) and two specimens from TU 1048 (one from the Tulane collection and one from the Schmelz collection).

Discussion: Turbo chipolanus is the more common of the two new species from the Chipola Formation. This species has no counterpart among fossil forms but is most similar to the rare Recent *Turbo haraldi* Robertson, 1957, which is described and figured by Abbott (1974, p. 58, text-fig. 478). Both *Turbo chipolanus* and *Turbo haraldi* are similar in size, have planate protoconchs, are imperforate and possess smooth body whorls. The major difference between the two species is that *Turbo haraldi* has two carinae on the early postnuclear whorls (*versus* one for *Turbo chipolanus*) with the upper one bearing short, flattened spines. According to Abbott (1974, p. 58) *Turbo haraldi* lives on gravel and sponge bottom in tropical and subtropical waters from the Bahamas to Panama.

Subgenus TAENEATURBO Woodring, 1928

Taeneaturbo WOODRING, 1928, Carnegie Inst. Washington, Publ. 385, p. 408.

Type species: *Turbo canaliculatus* Hermann, 1781, by original designation.

TURBO (TAENEATURBO) PACTILIS Schmelz, n. sp.
Plate 1, figure 3

Description: Shell medium-sized, thin, turbinate in form, imperforate. Protoconch submerged, about two whorls. Postnuclear whorls about five; suture distinct with an adjacent deep

channel at adapical end of penultimate and body whorl. Aperture severely damaged in all specimens, probably oval in shape. Teleoconch whorls rounded, sculptured with numerous, well-developed, beaded spiral costae of approximately equal size. Spiral costae separated by evenly spaced spiral grooves. Beaded pattern caused by oblique growth lines crossing over costae and grooves. Well-preserved fragments with vertical, wavy, dark and light bands extending across whorls.

Holotype: USNM 484400; height 27.0 mm, maximum diameter 23.2 mm.

Type locality: TU 555, Chipola Formation, east bank of Chipola River, about 1,000 feet above Fourmile Creek (SW 1/4 Sec. 29, T1N, R9W), Calhoun County, Florida.

Additional unfigured paratypes: One incomplete specimen from TU 547 (Tulane collection) and three fragments from TU 1048 (Tulane collection).

Discussion: Turbo pactilis is an extremely rare species with only one nearly complete specimen available for examination. Among fossil forms it bears some similarity to *Turbo dominicensis* Gabb, 1873 (p. 242; figured by Pilsbry, 1922, pl. 42, figs. 16, 17), from the Mio-Pliocene Cercado Formation of the Dominican Republic. It differs, however, from this species in that it has a submerged rather than planate protoconch, possesses conspicuous, nearly equal-sized, beaded cords over each teleoconch whorl, lacks the prominent beaded spiral cord just below the suture, and has a deep channel next to the suture on the penultimate and body whorl. Among extant forms *T. pactilis* is most like *Turbo canaliculatus* Hermann, 1781 (figured and described in Abbott, 1974, p. 58, pl. 2, text-fig. 475). However, *T. pactilis* differs from *T. canaliculatus* by the fact that it has a much narrower channel next to the suture and much more prominent beaded spiral cords covering the teleoconch whorls.

ACKNOWLEDGMENTS

This investigator would like to extend a special note of thanks to Emily Vokes for the loan of Tulane specimens and her assistance with photographic work. An additional note of appreciation is also extended to Mr. Burt Hayes for granting permission to collect on his property.

LOCALITY DATA

The following Tulane University localities are all in the Chipola Formation, Calhoun County, Florida:

547. West bank of Chipola River, about 2,000 ft. above Fourmile Creek (SW 1/4 Sec. 29, T1N, R9W).
555. East bank of Chipola River, about 1,000 ft. above Fourmile Creek (SW 1/4 Sec. 29, T1N, R9W).
1048. Farley Creek, south bank, about 0.8 mile east of bridge of Florida Highway 275 (NE 1/4 Sec. 21, T1N, R9W).

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November 15, 1995

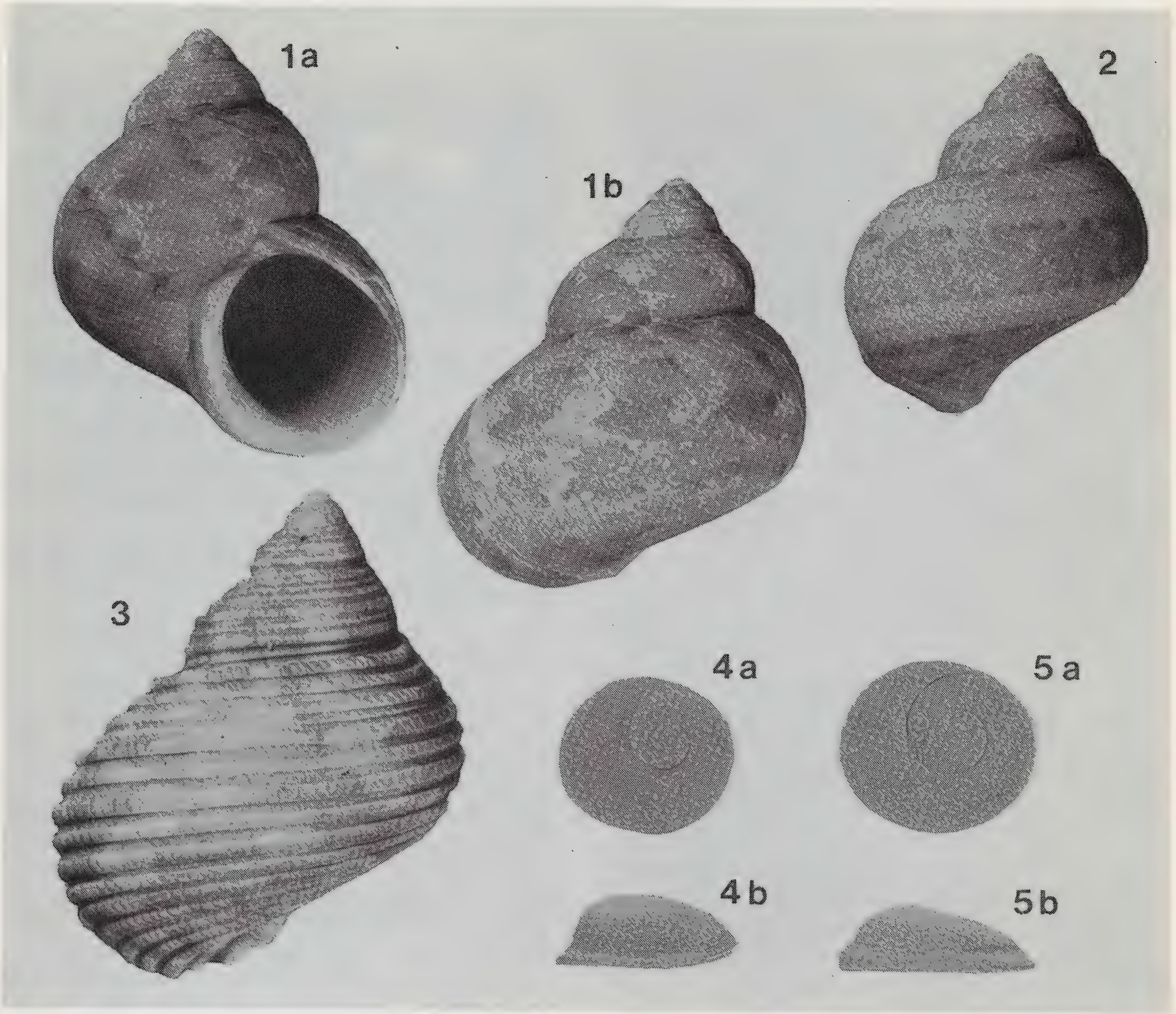

PLATE 1

Figures

1, 2. *Turbo (Halopsephus?) chipolanus* Schmelz, n. sp. (X2)
   1. USNM 484398 (holotype); height 19.4 mm, diameter 16.4 mm.
      Locality: TU 555, Chipola Formation, Florida.
   2. USNM 484399 (paratype); height 22.6 mm, diameter 19.0 mm.
      Locality: TU 555, Chipola Formation, Florida.

3. *Turbo (Taeneaturbo) pactilis* Schmelz, n. sp. (X2)
   USNM 484400 (holotype); height 27.0 mm, diameter 23.2 mm.
   Locality: TU 555, Chipola Formation, Florida.

4, 5. *Turbo* opercula (X2)
   4. USNM 484401; maximum diameter 9.5 mm.
      Locality: TU 555, Chipola Formation, Florida.
   5. USNM 484402: maximum diameter 10.5 mm.
      Locality: TU 1048, Chipola Formation, Florida.

NOTES ON THE FAUNA OF THE CHIPOLA FORMATION–XXXIX A NEW SPECIES OF THE GENUS *PARAMETARIA* (GASTROPODA:COLUMBELLIDAE)

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Not a great deal appears to be known about the genus *Parametaria* Dall, 1916. According to Jung (1994, p. 16) this genus has never been studied in detail. Reeve (1859) was the first investigator to describe these cone-like gastropods in his monograph on the genus *Meta*. In his presentation he noted that the members of this genus possess external morphological features that are intermediate in character between Swainson's two genera *Strombоidea* and *Conella*. In a subsequent study of the American Columbellidae, Dall (1916, p. 25) noted that the generic name *Meta* is preoccupied and proposed that it be replaced with *Parametaria*.

To date, only seven species of *Parametaria* have been described from the fossil record. Two come from the Miocene deposits of the Dominican Republic. These include *P. lopezana* Jung (1994, p. 19, pl. 7, figs. 4-9) from the late early to early middle Miocene deposits of the Baitoa Formation and *P. islahispaniolae* (Maury, 1917, p. 94, pl. 15, figs. 4, 5) from the late Miocene deposits of the Cercado and Gurabo formations. An additional two species have been unearthed from the Pliocene deposits (Jung, 1994, p. 16) of the Springdale Formation in Trinidad. These species are *P. prototypus* (Guppy, 1867, p. 171) and *P. schideri* (Rutsch, 1942, p. 148, pl. 5, figs. 5a, 5b). Of the remaining three species, *P. hertweckorum* Petuch (1991, p. 37, pl. 6, figs. 1, 2) and *P. lindae* (1986, p. 406, pl. 3, figs. 9, 10) come from the Pliocene Pinecrest Beds of Florida and *P. rutschi* Jung (1969, p. 500, pl. 52, figs. 3-6) from the Pleistocene deposits (Jung, 1994, p. 16) of the Talparo Formation of Trinidad.

No living forms of *Parametaria* have been discovered off the coast of Florida nor have any been found in the Caribbean. However, there is one living representative of this genus, *P. dupontii* (Kiener, 1849), which survives in the eastern Pacific Panamic Province from the Gulf of California to Tres Marias Islands on the west coast of Mexico (Keen, 1971, p. 598), making the genus yet another Paciphile.

At no time during their short geologic history do the members of this genus appear to be abundant (Jung, 1994, p. 16). In addition, the distribution of this rare form appears to be limited to tropical and subtropical shallow patch-reef environments, a fact that is substantiated by recent discoveries of a new species of *Parametaria* from shallow back-reef facies of Chipola Formation deposits along Farley Creek.

Family COLUMBELLIADE Swainson, 1840

Genus PARAMETARIA Dall, 1916

Parametaria DALL, 1916, Nautilus, v. 30, no. 3, p. 25, new name for *Meta* Reeve, 1859, not Koch, 1835.

Type species: *Conus dupontii* Kiener, 1849, by original designation.

Subgenus PARAMETARIA s. s.

PARAMETARIA (PARAMETARIA) BELLA Schmelz, n. sp.

Text-figures 1, 2

Description: Shell small, conical in form. Protoconch glossy, about two whorls; postnuclear whorls six. First two postnuclear whorls smooth and small. At fourth postnuclear whorl apical angle increasing markedly and whorls become wider and shouldered. A well-developed suture between last three whorls and numerous, faint, slightly raised growth lines crossing shoulders of each whorl. Near aperture, posterior half of body whorl arching sharply towards apex, creating a narrow anal canal. On anterior half of body whorl, siphonal canal sculptured with fine spiral cords. Aperture wide at the base and narrow at posterior end. Inner lip with thin callus extending to base of columella, the lower part containing seven small pustules. Outer lip folded inward, on inner margin about nine to twelve well-developed denticles.

Holotype: USNM 484396; height 11.0 mm, maximum diameter 5.9 mm.

Type locality: TU 825, Chipola Formation, Farley Creek at abandoned mill about 1/4 mile west of bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W), Calhoun County, Florida.

Paratype: USNM 484397; height 10.9 mm, maximum diameter 5.9 mm; locality TU 825, Farley Creek, Calhoun County, Florida.

Additional unfigured paratypes: Sixteen specimens from TU 825 (14 from the Tulane collection and two from the Schmelz collection); three specimens from TU 999 (two from the Tulane collection and one from the Schmelz collection);

three specimens from TU 819 (Schmelz collection) and one specimen from TU 1048 (Schmelz collection).

Discussion: Parametaria bella is the oldest member of this genus reported in North America and is comparable in age to *P. lopezana* Jung (1994, p. 16, pl. 7, figs. 4-9), which was described from the early and middle Miocene deposits of the Baitoa Formation, Dominican Republic. Its general shell morphology is most like *P. prototypus* (Guppy, 1867, p. 171) from the Pliocene Springdale Formation deposits in Trinidad. Similar to *P. prototypus, Parametaria bella* possesses a glossy protoconch of about two whorls followed by six teleconch whorls. In both species the apical angle increases markedly at the fourth postnuclear whorl, at which point the whorls become wider and more shouldered. *Parametaria bella* differs from its Trinidad counterpart in that it is a shorter and more slender shell (11.0 x 5.9 mm *vs.* 12.2 x 7.8 mm), and the apical angle of the spire formed by the expanded four teleconch whorls is less acute. *Parametaria bella* is probably the ancestor of *P. hertweckorum* Petuch (1991, p. 37, pl. 6, figs. 1, 2), which is fairly abundant in the Pliocene Pinecrest beds of Florida.

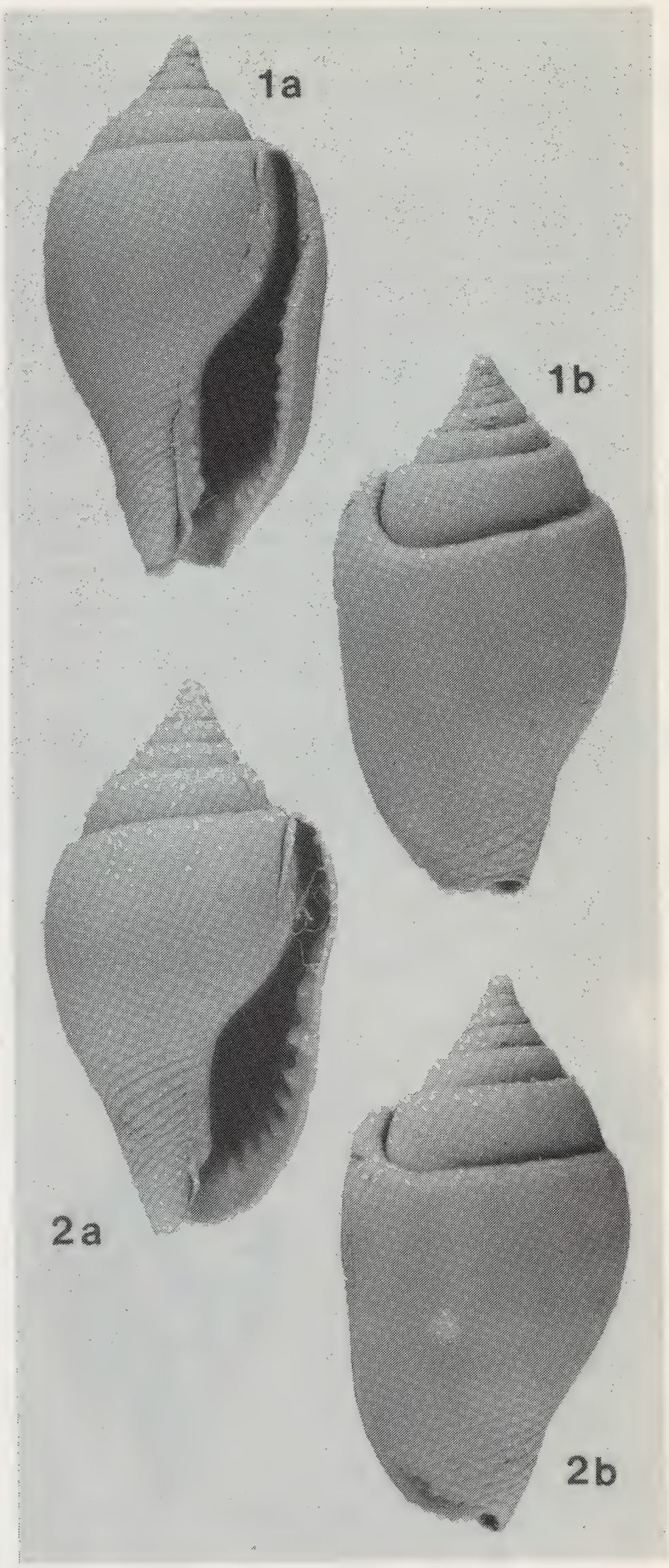
ACKNOWLEDGMENTS

This investigator would like to extend a special note of thanks to Emily Vokes for the loan of Tulane specimens and her assistance with the photographic work. An additional note of appreciation is also extended to Mr. Burt Hayes for granting permission to collect on his property.

LOCALITY DATA

The following Tulane University localities are all in the Chipola Formation, Calhoun County, Florida:

819. Farley Creek, 0.2 mile west of bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W).
825. Farley Creek at abandoned mill about 1/4 mile west of bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W).
999. Farley Creek, about 300 yards downstream from bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W).
1048. Farley Creek, south bank, about 0.8 mile east of bridge of Florida Highway 275 (NE 1/4 Sec. 21, T1N, R9W).



Text-figures 1, 2. *Parametaria (Parametaria) bella* Schmelz, n. sp. (X5). 1, USNM 484396 (holotype); height 11.0 mm, diameter 5.9 mm; locality TU 825, Chipola Formation, Florida. 2. USNM 484397 (paratype); height 10.9 mm, diameter 5.9 mm; locality TU 825, Chipola Formation, Florida.

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November 15, 1995

TWO ADDITIONS TO THE CENOZOIC MURICINAE (GASTROPODA:MURICIDAE) OF THE WESTERN ATLANTIC REGION

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It should be an axiom of systematic paleontology that there is never a *complete* catalogue of any group. This is certainly the case in the Cenozoic Muricinae, where only recently a updated study, with additions and corrections (Vokes, 1990, 1992) has been presented. No sooner were these revisions published than two additional, unusually spectacular species were discovered. As there are no plans for another revision in the foreseeable future, these two species are described.

Family MURICIDAE Rafinesque, 1815
Subfamily MURICINAE Rafinesque, 1815
Genus CHICOREUS Montfort, 1810

Chicoreus MONTFORT, 1810, Conchyl Syst., v. 2, p. 611.

Type species: *Murex ramosus* Linnaeus, 1758, by original designation.

Discussion: Houart (1992) has separated the genus *Chicoreus* into two subgenera: *Chicoreus* s.s., characterized by having a labral tooth, and *Triplex* Perry, 1810, lacking such a tooth. This division works well in the Indo-Pacific but it does not transfer to the western Atlantic. Those species that I assigned to the group of *C. brevifrons* in the aforementioned revision (Vokes, 1990, p. 33) have a much greater morphologic similarity to the strict subgenus than to the members of *Triplex*. The only thing they lack is the labral tooth. I find it difficult to place these American species in the subgenus *Triplex;* therefore, pending Mr. Houart's anticipated study of the Atlantic species of *Chicoreus* they simply will be assigned to the genus *Chicoreus* s.l.

In the stratigraphic record there are no species of true *Chicoreus* (as opposed to the subgenera *Phyllonotus* and *Siratus*) known before the Burdigalian, when there is a virtual explosion of species in both the Old World and the New. In the New World, species of *Chicoreus* are widespread, occurring in the Chipola Formation (Florida), the Baitoa Formation (Dominican Republic), the Pirabas Formation (Brazil), and the Cantaure Formation (Venezuela), all thought to be of the same Burdigalian age. By the Middle Miocene there are several beautiful species in southern Australia (Muddy Creek Marl – Balcombian), indicating that the genus was probably worldwide, although we do not have the fossils to document this.

When I originally described the Chipola species *Chicoreus elusivus* (Vokes, 1974, p. 82, pl. 1, figs. 1-4) I suggested that it was most closely related to the living *C. brevifrons* (Lamarck, 1822), which first occurs in the geologic record in the Middle Miocene of the Gulf of Mexico area (Florida and Mexico; Vokes, 1990, p. 35), although the species does not occur there today.

However, with the discovery of *C. winifredae*, n. sp., in the Cantaure Formation, Venezuela, we may have a better candidate for the true predecessor of *C. brevifrons*, which more than likely developed in the Caribbean and only made a brief incursion into the Gulf during the Middle Miocene, for there is no record of the species in any Gulf formations after that time.

CHICOREUS WINIFREDAE Vokes, n. sp.
Plate 1, figure 1

Description: Shell with six teleoconch whorls preserved in the unique holotype; early whorls missing (broken and plugged in life). Earliest remaining axial ornamentation of eight or nine equi-sized ridges, becoming three varices and three knob-like intervarical nodes by third teleoconch whorl. Varices consisting of elaborately ramose processes, one longer at shoulder and a second just posterior to suture on spire whorls. Spiral ornamentation initially of three stronger cords alternating with weaker ones; additional spiral threads intercalated until surface of adult shell entirely covered by myriad spiral elements, varying in strength as primary and secondary cords, and tertiary threads. Original strongest cords gradually developing into broad, low spiral ridges, giving rise at varices to ramose spines, with a small projection along edge of spine at each spiral thread. On body whorl one large spine at shoulder, with four smaller spines anterior to shoulder on body portion, and an additional two spines on siphonal canal. In addition to major spines, where secondary spiral cords cross varices, numerous shorter spinelets produced. Suture somewhat appressed. Aperture ovate, inner lip narrow, smooth, appressed at posterior end, free-standing at anterior end. At posteriormost portion a strong anal ridge

combining with edge of outer lip to form an anal notch. Inner side of outer lip with several paired lirations; outer margin crenulated in harmony with spiral ornamentation: cords producing grooves, areas between cords producing forward-directed points. Siphonal canal moderately long, broad, recurved at distal end. Previous terminations of canal forming a small fasciole.

Holotype: Naturhistorisches Museum Basel H-17655; height 70.0 mm, diameter 40.4 mm.

Type locality: NMB 17516, Cantaure Formation; series of arroyos about 500 meters south of "Casa Cantaure," which is 14 km (by road) west of Pueblo Nuevo, Paraguaná Peninsula, Venezuela.

Discussion: From 1972 to 1982, Mr. and Mrs. Jack Gibson Smith, then of Caracas, Venezuela, now of Surrey, England, collected the Cantaure fauna of the Paraguaná Peninsula, Venezuela. Upon their return to England, they donated their entire collection to the Naturhistorishes Museum, Basel, from where Peter Jung kindly forwarded to me the type specimen of this new species. It was collected by Mrs. Winifred Gibson Smith, December 23, 1977, and it gives me great pleasure to name this species in her honor.

The Gibson Smiths provisionally identified the specimen as "*Chicoreus* aff. *brevifrons*" and this is indeed the species to which it has the closest resemblance. Both *C. brevifrons* and *C. winifredae* differ from the superficially similar appearing contempory *C. elusivus* in that the latter has a total of six varical spines (one large and five small) on each body whorl varix. The other two have one large and four smaller spines, although in *C. brevifrons* the secondary spine adjacent to the shoulder spine often becomes almost as large as the shoulder spine, making this species immediately recognizable whenever seen (see pl. 1, fig. 2). It is this latter trait of *C. brevifrons* that is the principal character distinguishing *C. winifredae* from *C. brevifrons*. In *C. winifredae* the four anterior spines are all approximately the same size. Between the shoulder spine and the next spine anterior to it in *C. brevifrons* there is a relatively strong secondary spiral cord that gives rise to a smaller spinelet between these two larger spines. There is no such intercalary cord or spine in *C. winifredae*. Also, *C. brevifons* is a more triangular shell, much expanded at the shoulder. In contrast, *C. winifredae* has a more elongate outline.

Genus ASPELLA Mörch, 1877

Aspella MÖRCH, 1877, Malak. Blatter, v. 24, p. 24.

Type species: *Ranella anceps* Lamarck, 1822, by monotypy.

Discussion: The genus *Aspella* first occurs in the Oligocene of Dax, France, and does not appear in the New World before the Early Pliocene, with a Recent species, *A. castor* Radwin and D'Attilio, 1976, reported from the Gurabo Formation of the Dominican Republic (Vokes, 1989, p. 58, pl. 7, fig. 12).

In Florida, the Recent species *Aspella senex* (Dall, 1889) is rare in the Middle Pliocene Pinecrest beds (Vokes, 1975, p. 132) but becomes slightly more abundant in the younger Caloosahatchee and Bermont formations. This species is not ever widely collected, due to its small size (maximum height under 15 mm).

Petuch has figured two specimens identified as *A. castor* and *A. senex* (1994, pl. 43, figs. L and Q, respectively), the first said to be from "Unit 10" and the second from "Unit 7" at the APAC pit, Sarasota, Florida (= locality TU 1000). The specimen of "*A. castor*" is just a small example

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PLATE 1

1. *Chicoreus winifredae* Vokes, n. sp. (X 1 1/4)
   NMB H-17655 (holotype); height 70.0 mm, diameter 40.4 mm.
   Locality: NMB 17516, Paraguaná Peninsula, Venezuela; Cantaure Formation.
2. *Chicoreus brevifrons* (Lamarck, 1822) (X 1 1/4)
   Vokes Collection; height 70.0 mm, diameter 48.0 mm.
   Locality: Paraguaná Peninsula, Venezuela, under rocks at low tide; Recent.
3. *Aspella petuchi* Vokes, n. sp. (X 3)
   USNM 842064 (holotype); height 25.3 mm, diameter 10.7 mm.
   Locality: TU 1000, Sarasota, Florida; Pinecrest beds.

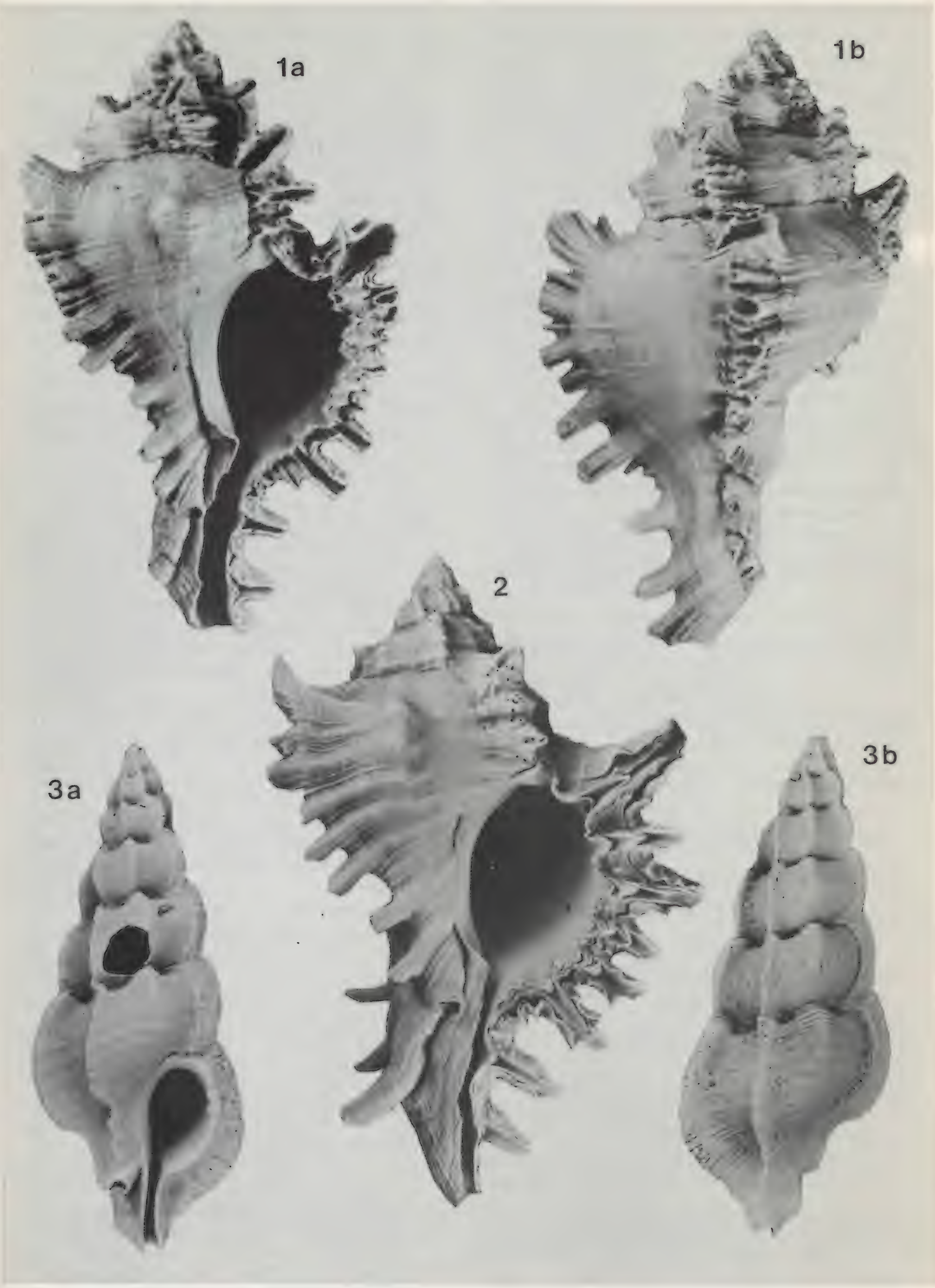

PLATE 1

of *A. senex* but the specimen of "*A. senex*" is more slender and is probably another example of the species described below. The holotype of this new species was collected by Dr. Petuch from "Unit 7" at APAC, and identified by him as "*A. senex*."

ASPELLA PETUCHI Vokes, n. sp.
Plate 1, figure 3

Description: Lanceolate shell, large for the genus; seven teleoconch whorls, protoconch missing. Axial ornamentation on first four teleoconch whorls of six equally rounded ridges; by fifth whorl two of these on opposite sides of shell becoming stronger, forming narrow strap-like varices, giving a dorso-ventral flattening to shell. Other ridges remaining as intervarical swellings, two between each pair of varices, that one located abaperturally to each varix stronger than the other. Varical margins gently rounded except at base of body whorl where a small incurving breaks simple curved line. Only faint spiral cords, about five on body whorl, otherwise shell smooth between axial ornamentation. In life shell covered by a thick chalky intritacalx, when worn displaying a network of fine spiral tubes. Suture impressed, crossed by buttresses formed at apical end of intervarical ridges. Aperture small, oval, no anal notch; inner lip smooth, appressed entire length. Inner side of outer lip with about eight small denticles. Siphonal canal short, broad, slightly recurved at distal end; termination of previous canal diverging as a spur beside present canal.

Holotype: USNM 842064; height 25.3 mm, diameter 10.7 mm.

Type locality: TU 1000, Pinecrest beds; APAC pits at east end of 17th St., about 8 miles east of U.S. Highway 301 [now northwest of Fruitville Rd. exit, I-75], at Sarasota (T36S, R19E), Sarasota Co., Florida.

Discussion: Although identified as *A. senex* by Petuch, this species differs in the more elongate outline and the larger size. In general outline it is more similar to the eastern Pacific *A. pyramidalis* (Broderip, 1833), which is also generally a smaller shell (although Radwin and D'Attilio, 1976, p. 23, give 21 mm as a maximum size and figure one shell [pl. 1, fig. 5] about 19 mm, under 15 mm seems to be the "normal" size for the species). The intervarical buttresses are much more appressed in *A. pyramidalis* (see Vokes, 1975, pl. 1, fig. 13).

The three similar appearing species, *A. senex* and *A. castor* in the western Atlantic, and *A. pollux* Radwin and D'Attilio, 1976, in the eastern Pacific, are all marked by much more expanded varical flanges. The only western Atlantic species somewhat similar to *A. petuchi* is the small *A. cryptica* Radwin and D'Attilio, 1976 (usually under 10 mm in length; see Vokes, 1992, pl. 12, fig. 7), which differs in lacking the enlarged axial ridge adjacent to the varix seen in all of the other species mentioned.

The type specimen was collected by Dr. Edward J. Petuch at the APAC pit in 1990, and was presented to me by him. I am pleased to name this remarkable addition to the genus *Aspella* in his honor.

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November 15, 1995

A NEW SPECIES OF *ENAETA* (GASTROPODA:VOLUTIDAE) FROM THE MIO-PLIOCENE OF NORTHWESTERN ECUADOR

WILLIAM D. PITT[1,2] and LOIS J. PITT[2]

ABSTRACT

Two species of *Enaeta* occur in the Recent fauna of the Tropical East Pacific: *E. cumingii* (Broderip, 1832), and *E. barnesii* (Gray, 1825). The fossil record from the Tropical East Pacific is represented by *E. barnesii* from the Pleistocene of Panama, and a new species, *E. propecumingii* from the Miocene Angostura Formation and the Pliocene Esmeraldas beds, Onzole Formation, of northwestern Ecuador. The occurrence of *E. propecumingii* in the Angostura Formation is the oldest known fossil record of the genus *Enaeta* in the Tropical East Pacific.

INTRODUCTION

The genus *Enaeta* Adams and Adams, 1853, which has sometimes been considered a subgenus of *Lyria* (Keen, 1971, p. 619; Hoerle and Vokes, 1978, p. 106), is a New World genus (Woodring, 1964, p. 289; Abbott, 1974, p. 245; Skoglund, 1992, p. 94) represented by five species in the western Atlantic fossil record, with *E. isabellae* (Maury, 1910, p. 17) from the late Lower Miocene Chipola Formation of Florida the earliest recorded occurrence. Other species included are: *E. trechmanni* Jung (1971, p. 201), from the Middle Miocene Grand Bay Formation, Carriacou, West Indies; *E. perturbatrix* (Maury, 1917, p. 76), from the Mio-Pliocene Gurabo Formation, Dominican Republic; and two species from the Pliocene Gatun Formation, Panama: *E. economia* (Woodring, 1964, p. 289) and *E. olssoni* Hoerle and Vokes (1978, p. 116). The eastern Pacific has two known fossil species: *E. barnesii* (Gray, 1825), a Recent species that also occurs in the Pleistocene beds of the Burica Peninsula, Panama, and *E. propecumingii*, n. sp. The genus *Enaeta* is represented in the Recent western Atlantic by three species: *E. cyllenifor-mis* (Sowerby, 1844, p. 151), Florida to Brazil; *E. guildingi* (Sowerby, 1844, p. 151), Antilles to Brazil; and *E. reevei* (Dall, 1907, p. 353), Cuba to Honduras. There are two species in the Recent Tropical East Pacific: *E. cumingii* (Broderip, 1832, p. 33), and *E. barnesii* (Gray, 1825, p. 511); both occur from the Gulf of California to Peru.

Enaeta propecumingii, n. sp., from the Late Miocene Angostura Formation of northwestern Ecuador, is the earliest known fossil record of the genus *Enaeta* in the Tropical East Pacific. The genus *Lyria* s.s. is known from older formations in the eastern Pacific, as far north as the state of Washington (Weaver, 1942) but not in the Tropical East Pacific.

In the geological record there are more species of the genus *Enaeta* in the western Atlantic than in the Tropical East Pacific and it is probable that the genus originated in the western Atlantic.

Abbreviations for Repository Institutions

CAS – California Academy of Sciences, San Francisco, California.

LACM – Los Angeles County Museum of Natural History, Los Angeles, California.

PRI – Paleontological Research Institution, Ithaca, New York.

TU – Tulane University, New Orleans, Louisiana.

USNM – United States National Museum of Natural History, Washington, DC.

ACKNOWLEDGMENTS

We want to thank Dr. Emily Vokes of Tulane University for help with the manuscript and for making available specimens from Tulane collections, including paratypes, and Allan Mc Makin, from Hammond, Oregon, for the photography.

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Cuvier, 1797
Class GASTROPODA Cuvier, 1797
Subclass PROSOBRANCHIA
Milne-Edwards, 1848

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Superorder CAENOGASTROPODA
Cox, 1959
Order NEOGASTROPODA Thiele, 1925
Superfamily MURICOIDEA
Rafinesque, 1815
Family VOLUTIDAE Rafinesque, 1815
Subfamily LYRIINAE
Pilsbry and Olsson, 1954
Genus ENAETA
H. Adams and A. Adams, 1853

Enaeta H. Adams and A. Adams, 1853, The Genera of Recent Mollusca, v. 1, p. 167.

Type species: *Voluta harpa* Barnes, 1824, by subsequent designation, Cossmann, 1899; Recent, eastern Pacific. [*Voluta harpa* Barnes, 1824, *non* Mawe, 1823 = *Voluta barnesii* Gray, 1825 (as *barnsii*)].

ENAETA PROPECUMINGII, n. sp.
Pitt and Pitt
Plate 1, figure 1

Description: Shell elongate, of medium size, with seven whorls; protoconch of about three, smooth, rounded whorls with a blunt ending. Spire whorls (ornamentation appearing immediately) evenly tapering, bearing two rows of nodes; one row of low nodes anterior to suture; a narrow smooth interspace; and one row of larger, elongated nodes just posterior to suture. Body whorl with a row of nodes anterior to the suture; narrow, smooth interspace, separating major axial sculpture, which consists of 11 to 13 smooth, rounded ribs, extending from interspace to base of shell. Aperture elliptical, more than one-half of shell height; outer lip thickened, with a small blunt tooth midway on inner side of outer lip. Columellar wall with three strong plications anteriorly, and three faint plications, evenly spaced posteriorly. Anterior canal recurved.

Etymology: From the Latin, *prope* meaning near and *cumingii* from the Recent *E. cumingii* (Broderip, 1832).

Holotype: CASG 67695.01; height 29.6 mm, diameter 14.3 mm (Plate 1, fig. 1).

Type locality: P-101, Esmeraldas beds, road cut (south side), immediately west of the village of Camarones, about 20 km (by road) east of the bridge over Rio Esmeraldas, Esmeraldas Prov., Ecuador (= TU 1399).

Paratype A: CASG 67695.02; height 31.4 mm, diameter 14.9 mm; locality TU 1397, Esmeraldas beds, Ecuador.

Paratype B: CASG 67695.03; height 24.2 mm, diameter 13.5 mm; locality P-103, Angostura Formation, Ecuador.

Paratype C: USNM 484521; height 26.0 mm, diameter 13.7 mm; locality P-101, Esmeraldas beds, Ecuador.

Paratype D: USNM 484522; height 19.5 mm, diameter 8.8 mm; locality TU 1399, Esmeraldas beds, Ecuador.

Paratype E: PRI 33194; height 17.9 mm, diameter 9.2mm; locality TU 1399, Esmeraldas beds, Ecuador.

Paratype F: LACMIP 12298; height 20.9 mm, diameter 10.7 mm; locality TU 1399, Esmeraldas beds, Ecuador.

Occurrence: Angostura Formation and Esmeraldas beds of the Onzole Formation, Ecuador.

Discussion: Enaeta propecumingii, n. sp., is represented by eight specimens, three from locality P-101, three from locality TU 1399, one from locality TU 1397 and one from locality P-103. The fossil specimens examined are most similar to the fossil *E. trechmanni* Jung, 1971, and the Recent *E. cumingii* (Broderip, 1832). *Enaeta trechmanni* differs in having a somewhat globose, but evenly tapering spire and 18 axial ribs rather than the slender, evenly tapering spire and approximately 12 axial ribs of *E. propecumingii*. The body whorl of *E. trechmanni* does have a row of nodes anterior to the suture, a narrow smooth interspace, and axial ribs extending from the interspace to the base of the shell; thus, becoming the closest species to *E. propecumingii* in the fossil record. *Enaeta propecumingii* is also similar to the Recent *E. cumingii* but the latter has only a single row of nodes about midway on the spire whorls, in contrast to two rows in *E. propecumingii*. *Enaeta cumingii* also differs in that the body whorl has a smooth interspace anterior to the suture, a row of nodes and nine axial ribs extending to the base of the shell with a secondary row of nodes at their mid-point.

The Recent *E. cumingii* apparently arose in the Tropical East Pacific from *E. propecumingii*.

LOCALITY DATA

The following are Pitt localities:

P-101. Esmeraldas beds, road-cut (south side), immediately west of the village of Camarones, about 20 km (by road) east of the bridge over Río Esmeraldas, Esmeraldas Prov., Ecuador.

P-103. Angostura Fm., sea cliffs about 300 meters west of Punta Verde, about 2 1/4 km east of the mouth of Río Verde and about 22 km east of the bridge over Río Esmeraldas, Esmeraldas Prov., Ecuador.

PLATE 1

Figures

1. *Enaeta propecumingii* Pitt and Pitt, n. sp.
   CASG 67695.01 (holotype); height 29:6 mm, diameter 14.3 mm (X 1.8).
   Locality: P-101, Esmeraldas beds, Ecuador.
2. *Enaeta cumingii* (Broderip, 1832)
   CASIZ 099363; height 33.2 mm, diameter 17.0 mm (X 1.4).
   Locality: PR-100, San Carlos Bay, Guaymas, Sonora, Mexico; Recent.

PR-100. Recent, San Carlos Bay, Guaymas, Sonora, Mexico.

The following are Tulane University localities:

1397. Esmeraldas beds, Quebrada Camarones, cut-bank on east side of canyon, which is at east edge of village of Camarones, 20 km (by road) east of bridge over Río Esmeraldas, or approximately 10 km east of mouth of Río Esmeraldas, Esmeraldas Prov., Ecuador.

1399. Esmeraldas beds, road-cut on west side of village of Camarones, which is 20 km (by road) east of bridge over Río Esmeraldas, at Esmeraldas, Esmeraldas Prov., Ecuador.

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November 15, 1995

PALEONTOLOGICAL NOTES

NOTES ON CERTAIN SPECIES OF MOLLUSCA FROM THE WACCAMAW FORMATION OF SOUTH CAROLINA, SAID TO BE FROM THE PINECREST FORMATION OF FLORIDA, AND *VICE VERSA*

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In a recent publication Petuch (1994) figured three specimens as species described by Olsson and Petit, 1964, accompanied by notations that the original locality was incorrect. According to Petuch these are:

"*Scaphella brennmortoni* Olsson and Petit, 1964. Length 141 mm. PB – specimen from Petuch Unit 7, APAC pit, Sarasota, Sarasota Co. Erroneously stated as coming from South Carolina, this is actually a Pinecrest Beds species (*fide* R.E. Petit, pers. comm.)". – Petuch, 1994, p. 196, pl. 77, fig. H (not in text).

This is not only a Waccamaw species but it is one of the more common large gastropods of the Waccamaw Formation. Specimens are on hand and available had Dr. Petuch inquired. This species was never mentioned in conversations between us.

The specimen figured by Petuch, stated to be from Sarasota, Florida, is shown only in a reduced size dorsal view. Although it appears to be conspecific with *S. brennmortoni* it is suggested that Florida and South Carolina specimens be physically compared.

"*Conus (Leptoconus) presozoni* Olsson and Petit, 1964. Length 112 mm. PB – specimen from Petuch Unit 7, APAC pit, Sarasota, Sarasota Co. Originally described as coming from the Waccamaw Formation of Myrtle Beach, South Carolina (a mistake) but now known to be confined to the Pinecrest Beds of southern Florida (*fide* R.E. Petit, pers. comm.)." – Petuch, 1994, p. 226, pl. 92, fig. A (not in text).

This species is most definitely a Waccamaw species, and paratypes are on hand that could have been made available to Petuch had he inquired. This species was never mentioned in conversations between us. Petuch previously (1991, p. 52) referred to *C. presozoni* as being from "both the Duplin Formation of South Carolina and the 'Pinecrest Beds' of southern Florida." This is the only report of this species from the Duplin Formation and in the absence of specific locality data is meaningless. It is not possible to determine whether or not the specimen figured by Petuch is *C. presozoni*. Specimens from Florida need to be compared with specimens from the Waccamaw Formation.

"*Conus (Lithoconus) cherokus* Olsson and Petit, 1964. Length 71 mm. PB – specimen from Petuch Unit 7, APAC pit, Sarasota, Sarasota Co. Originally described as coming from the Waccamaw Formation of Myrtle Beach, South Carolina (a mistake) but now known to be confined to the Pinecrest Beds of southern Florida (*fide* R. E. Petit, pers. comm.)." – Petuch, 1994, p. 228, pl. 93, fig. A (not in text).

In this instance Petuch is correct, as this is a Pinecrest species. Somehow the wrong locality was put on the type specimen. For our 1964 paper, Dr. Olsson photographed all of the specimens, prepared the plates, and also did the great majority of the writing. When I saw the portion of the manuscript describing this species, the type (only specimen known at the time) had already been sent to the National Museum. When I finally was able to get to Washington and examine the type it was found that it was not from the Waccamaw Formation but from the Pinecrest Formation, but the paper was already in press. Matrix was removed from the type and placed in a glass vial, which remains with the specimen. Macroscopic examination indicates that the matrix is not of Waccamaw origin, but matches that of Pinecrest material from Forty Mile Bend west of Coral Gables, Florida.

The fact that the type locality was incorrect was passed on verbally to many interested persons but this writer unfortunately never had occasion to write a paper in which a correction would be appropriate. When Dr. Petuch began working with the Florida Tertiary this information was passed on to him in a conversation. At some point he indicated that he would like

to include a correction of the type locality in one of his papers if I had no objection. He was told, of course, that a correction was needed and that he should publish it when appropriate. This appears to be the first correction although Petuch recognized the species as being Pinecrest in 1982 (p. 17) when he mentioned it as occurring in his Unit 6 of the Pinecrest.

It is embarrassing to have to admit to such a basic error as describing a new species from the wrong locality but the unfortunate fact is that this was done. However, to be accused of having done so on a wholesale basis is not acceptable. Being credited with interlocutory error is equally unacceptable. In telephone conversations after Petuch's book appeared he assured me that an errata sheet would be published in which he would retract his statements regarding *Conus presozoni* and *Scaphella brennmortoni*, and that the errata sheet would not only be placed in all copies of the work still unsold, but an effort would be made to make the availability of the errata sheet known to the paleontological community so that those already having a copy of the book could receive the errata sheet. To date this errata sheet has not appeared.

The temptation to go into a review of this latest of Petuch's books (1994) has been resisted as it would be hard to find a stopping place once started. It does seem appropriate here to issue a caveat to paleomalacologists that all references in this work to occurrences in the Waccamaw Formation need to be examined (*e.g*, *Cantharus olssoni* Petuch, n.sp., which on the plate caption is stated to be from "C[aloosahatchee]; Waccamaw Formation – holotype from Miami Canal dig, south of Lake Harbor, Palm Beach Co." but in the description the only locality given is for the Caloosahatchee. It is possible that this species does occur in the Waccamaw, but despite several decades of collecting Waccamaw material it has never been seen by this writer. This is true of some other species stated to be "Waccamaw" by Petuch.

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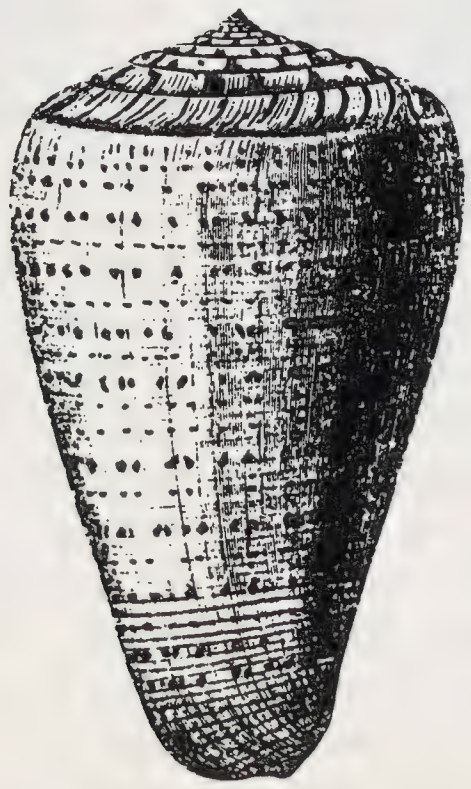

ON THE OCCURRENCE OF *STROMBINA CYPHONOTUS* AND *STROMBINA LESSEPSIANA* IN THE DOMINICAN REPUBLIC

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*ALBUFEIRA, PORTUGAL**

In the description of *Strombina lessepsiana* (Brown and Pilsbry, 1911, p. 352, pl. 25, figs. 11, 12) the authors compared their new species from the Gatun Formation with two as-yet undescribed species in the Gabb Collection from Santo Domingo. In order to demonstrate the relationship between these three species, in an extended footnote (Brown and Pilsbry, 1911, pp. 352-353) they published descriptions of these two new species extracted from "Johnson and Pilsbry's [*i.e.*, Pilsbry and Johnson, 1917] report on Gabb's Santo Domingo fossils (not yet published)." The species were cited correctly as Pilsbry and Johnson and were figured on pls. 25, figs. 6, 7 and 9, 10. When Pilsbry and Johnson (1917) was published there was no mention of these two species. In the final report (Pilsbry, 1922, p. 351) they are simply listed as having been described and figured in the Pilsbry and Johnson 1911 paper.

Although both species were mentioned by Maury (1917) as occurring in the Miocene of the Dominican Republic, no locality was given. Jung discussed these species in his study of the Dominican species of *Strombina* (1986, 1989) and, as no further specimens had been found to date, Jung concluded there probably had been an error and the specimens allegedly from the Neogene of the Dominican Republic originally had formed a single lot collected from the Gatun Formation of the Panama Canal Zone.

I had the opportunity to collect in the Dominican Republic in December, 1994, and February, 1995. The first of the two trips fortunately coincided with the end of the dry season, following an unusually dry rainy season. Consequently, the rivers were lower than normal, even for the dry season.

In December, 1994, on the west bank of the Río Yaque del Norte (north point of locality NMB 17265, text-fig. 21 of Saunders, Jung, and Biju-Duval, 1986; see text-figure 1), the lowest part of the river bed exposed grey silts extremely rich in mollusks, *Strombina* being the predominant gastropod genus. This locality falls within the Baitoa Formation, late Early Miocene (Saunders, Jung, and Biju-Duval, 1986). Twenty-three specimens of *S. cyphonotus* and five of *S. lessepsiana* were collected. On the second visit eight weeks later the beds were no longer exposed.

I have had the opportunity to compare the specimens of *S. lessepsiana* from the Dominican Republic with specimens from the type locality (Gatun Formation of Panama). The specimens originally described as *S. prisma* are undoubtedly conspecific with *S. lessepsiana*, as pointed out by Jung (1989, p. 66). Therefore, there are only two species: *S. lessepsiana*, of which *S. prisma* is a synonym, and *S. cyphonotus*. Both of these species occur in the Late Miocene Gatun Formation of the Panama Canal Zone.

The specimens of *S. cyphonotus* and *S. lessepsiana* collected from the Río Yaque del Norte are identical to those figured by Jung (1986, pls. 1-2) as doubtfully occurring in the Dominican Neogene. Although there are several features that tend to distinguish the two species (Jung 1986, pp. 11-12; 1989, p. 57), these are variable, only the longer anterior canal in *S. lessepsiana* consistently separates the two. This is the first time these two species have been reliably recorded with locality data confirming their occurrence in the Dominican Neogene.

I would like to thank Peter Jung, Naturhistorisches Museum, Basel, for his help and encouragement.

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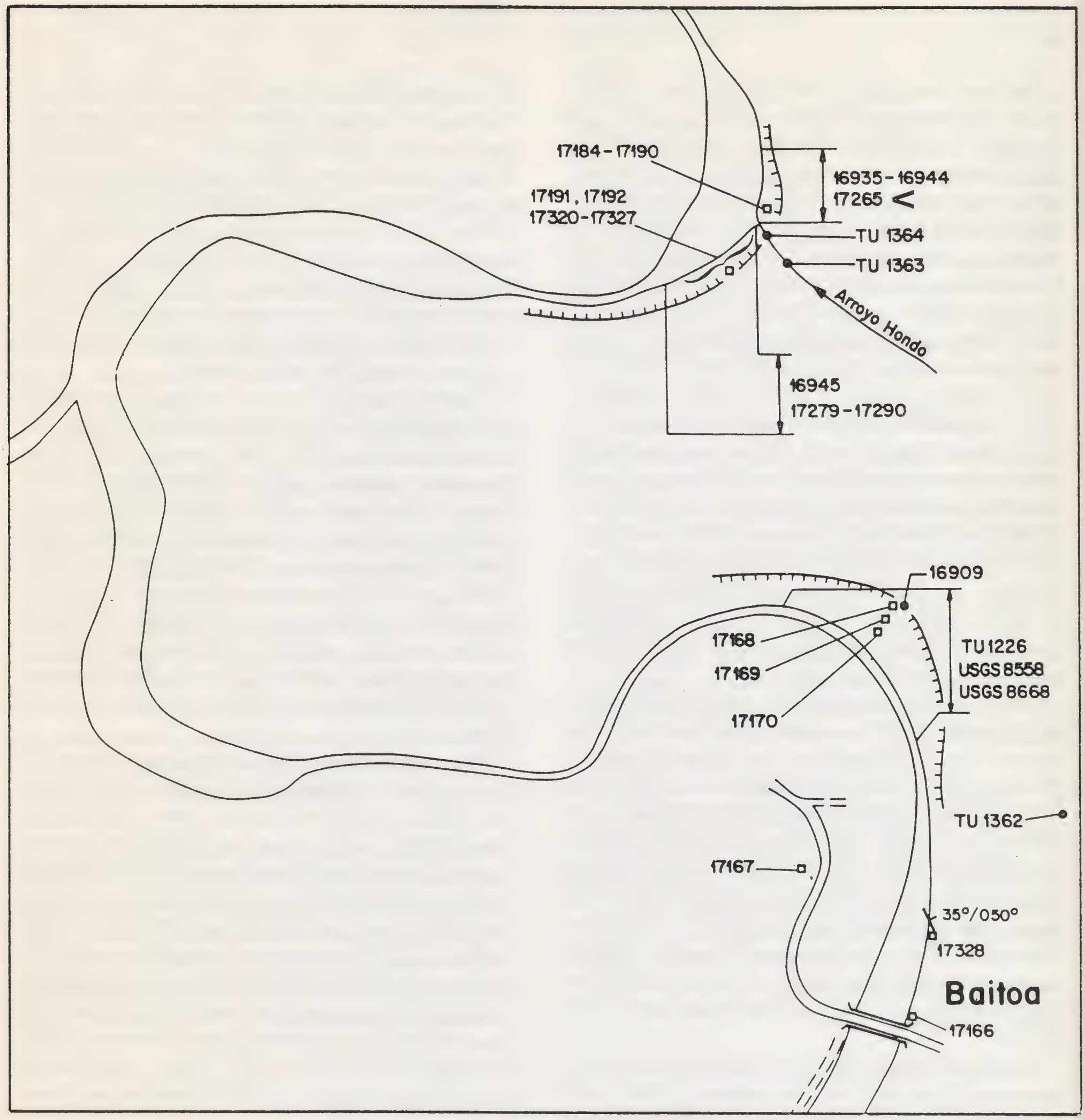

Text-figure 1. Map of Río Yaque del Norte, below the village of Baitoa, Dominican Republic (after Saunders, Jung, and Biju-Duval, 1986, text-figure 21).

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November 15, 1995

DISCOASTER PETALIFORMIS MOSHKOVITZ AND EHRLICK, 1984, *COINCIDENTALIS*, A NEW SUBSPECIES FROM THE SUBSURFACE OF LOUISIANA

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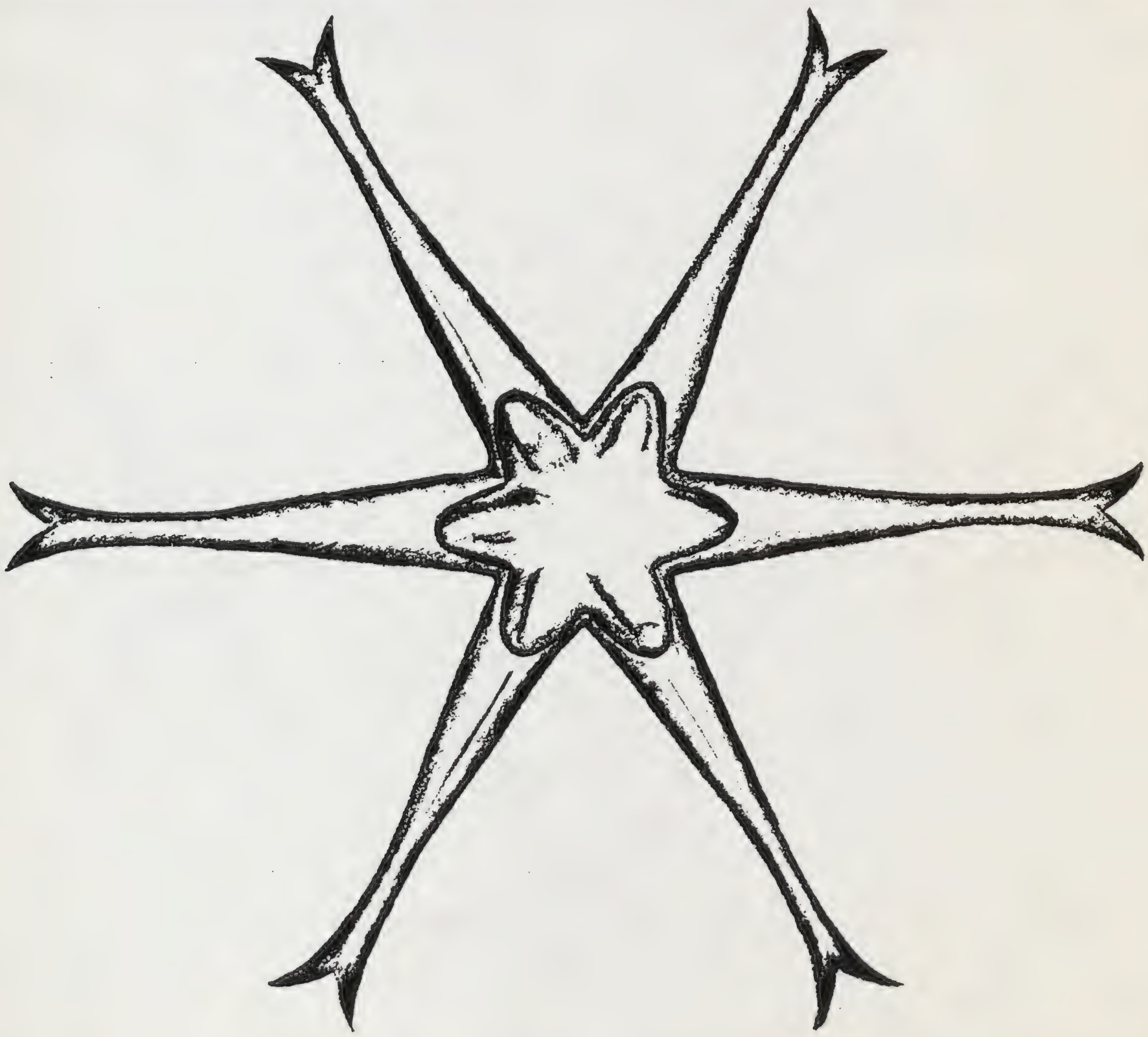
The purpose of this report is to delineate the range of a hitherto undescribed subspecies of *Discoaster* in the subsurface of the Louisiana Gulf Coast. The writer has found it useful for well-to-well correlation because of its short vertical range, which is the shortest of all calcareous nannoplankton and planktic foraminifera known to this author. The entire range is within Calcareous Nannofossil Zone 5, late Early Miocene (NN 5 = *Sphenolithus heteromorphus* Zone; see Tappan, 1980, table 9.4, Neogene biostratigraphic zonation based on calcareous nannoplankton). This subspecies has been identified from subsurface samples in the Shell Michel no. 1, 1-14S.-12E., Assumption Parish, Louisiana, 8395 to 8400 feet; the Mississippi River Fuel no. 3, State Lease no. 3403, Bay-23S.-15E., Pass Wilson Field, Terrebonne Parish, Louisiana; the Odeco-Murphy OCGS-5879, no. 2, Green Canyon Block 21, 12,540 to 12,570 feet; the Conoco no. 1, Mobile Area, Block 991; the Amoco no. 1, OCS-G-5956, North Padre 1008, 4980 to 5070 feet; and the Conoco no. 2, Mobile Area, Block 991, 4720 to 4930 feet. The last four occurrences were in ditch samples.

The author is grateful to his wife Beverly J. Pecunia, for illustrating the holotype, and to Joseph E. Boudreaux, New Orleans, Louisiana, for reading the manuscript and calling the writer's attention to the species of Moshkovitz and Ehrlick.



Text-figure 1. *Discoaster petaliformis* Moshkovitz and Ehrlick, 1984, *coincidentalis*, n. subsp., X 325.

SYSTEMATIC PALEONTOLOGY

Order DISCOASTERACEA Hay, 1977
Genus DISCOASTER Tan Sin Hok, 1927

DISCOASTER PETALIFORMIS Moshkovitz and Ehrlick, 1984
COINCIDENTALIS, new subspecies
Text-figure 1

Description: The subspecies typically has six rays with bifurcations forming an angle of forty-five degrees. The central knob is extremely high and is present on both distal and proximal sides. The knobs cover the central area and extend a short distance along the rays. They are also six-rayed but unbifurcated. The length of each ray is invariably twice the diameter of the central knob.

Holotype: USNM 487756; the longest dimension is along extremities of the opposing rays and is four microns.

Type locality: The holotype is from Odeco-Murphy, OCSG-5879, well no. 2, Green Canyon Block 21, at a depth of 12,540-12,570 feet.

Discussion: Most of the specimens figured by Moshkovitz and Ehrlick (1984, Unit 10, figs. 163-169) have rays that are only as long as the diameter of the central knob but some have rays twice the length of the diameter. The specimens observed in wells off the Louisiana Gulf Coast do not have this variation. Accordingly, the writer believes that the isolation of individuals in the Louisiana Gulf Coast Neogene from individuals in Israel gave rise to different gene pools for ray length. This difference indicates the validity of a geographic subspecies.

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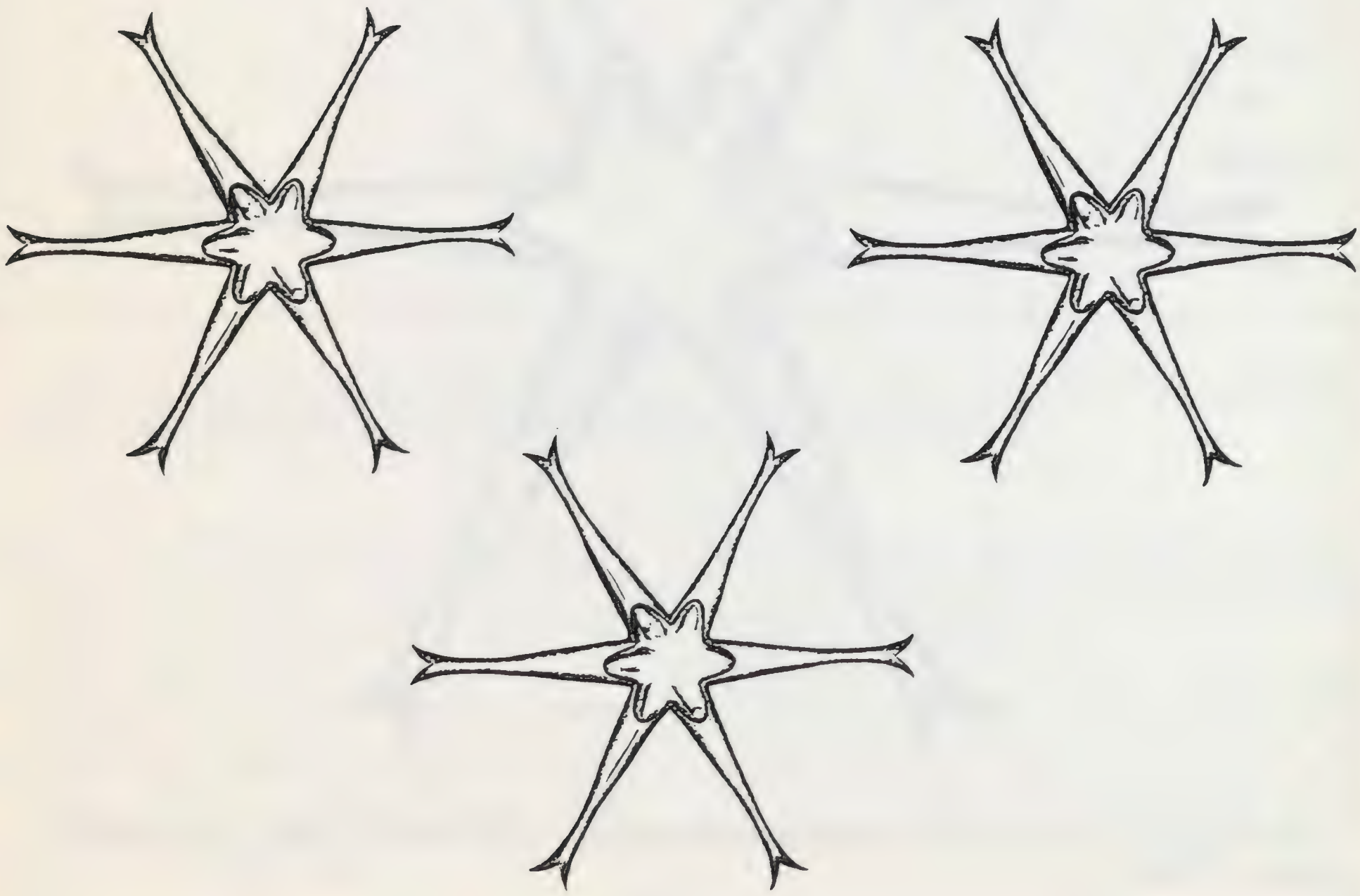

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